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# Occurrence of an exceptional catch of pelagic juvenile lingcod (*Ophiodon elongatus*) off Point Reyes, California

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## ABSTRACT

An exceptionally large catch of pelagic juvenile lingcod (*Ophiodon elongatus*) was made just offshore of Point Reyes, California in 1990. Results of 678 midwater trawls from annual surveys from 1983 to 1990 show that pelagic juvenile lingcod have a strong nearshore distribution and were most abundant in the Gulf of the Farallones, with a mean abundance of 5.0 per trawl. Otoliths from fish taken in the large catch were used to estimate parameters of a log-transformed Gompertz growth model, which was then used to calculate hatch dates. Hatching peaked around 24 March and ranged from 10 March to 19 April, implying a January–February spawning season for lingcod off central California. The large catch was associated with an anticyclonic eddy which would lead to water being trapped near the coast; convergence of fish associated with the eddy may have been due to either physical or biological effects.

**Key words:** anticyclonic eddy, larval abundance, lingcod, otoliths

## INTRODUCTION

Patchy spatial distributions are common in trawl surveys (Lenarz and Adams, 1980; Pennington, 1986) and are frequently most extreme in surveys of pelagic fishes (Smith and Hewitt, 1985). Here we report on the occurrence of an unusually large catch of pelagic juvenile young-of-the-year lingcod (*Ophiodon elongatus*) taken during a series of annual surveys conducted off central California. To estimate the hatch dates of the lingcod in this one catch we construct a growth model for the first 5 months of life. Local oceanographic features in the area at the time of the unusual catch are also described.

Lingcod have a complex form of reproduction (Cass *et al.*, 1990). In British Columbian waters, peak spawning occurs from January to February, after mature fish have migrated into shallow (< 30 m) rocky areas. Males establish territories and remain to guard a demersal egg mass until hatching is complete after 7 weeks. Larval lingcod hatch at a standard length (SL) of 7–9 mm and, while planktonic, undergo juvenile transformation at ≈20 mm SL. They remain pelagic until early summer, when they settle to benthic habitats at ≈70–80 mm SL.

## METHODS

Lingcod were collected incidentally during annual trawl surveys of pelagic juvenile young-of-the-year rockfish (*Sebastes* spp.). Since 1983, sampling has been conducted 1–4 times per year at a fixed series of stations off central California (Fig. 1, Table 1) using a 26 × 26 m

**Table 1.** Summary of midwater trawl surveys conducted for pelagic fishes off the central California coast (1983–90). See Wyllie Echeverria *et al.* (1990) for a detailed description.

| Year | Cruise | Dates Begin | Dates End | Number of hauls |
|---|---|---|---|---|
| 1983 | 1 | 8 June | 24 June | 21 |
| 1984 | 1 | 12 June | 27 June | 25 |
| 1985 | 1 | 5 June | 30 June | 30 |
| 1986 | 1 | 3 June | 25 June | 90 |
| 1987 | 1 | 10 April | 22 April | 35 |
| 1987 | 2 | 23 May | 21 June | 106 |
| 1988 | 1 | 16 April | 22 April | 29 |
| 1988 | 2 | 22 May | 18 June | 105 |
| 1989 | 1 | 14 May | 13 June | 100 |
| 1990 | 1 | 28 March | 6 April | 38 |
| 1990 | 2 | 13 May | 10 June | 99 |
| | | | Total | 678 |

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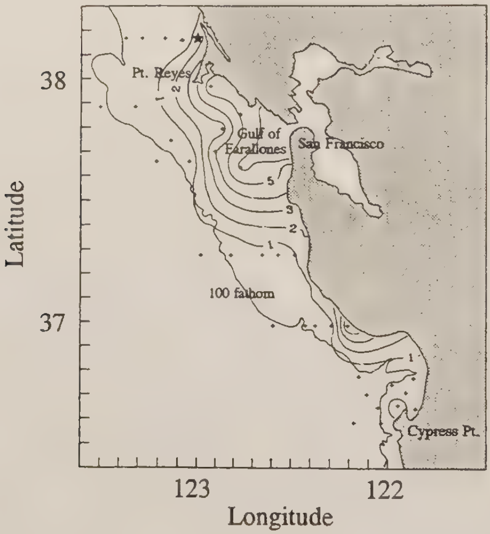
**Figure 1.** Spatial contours of the average number of lingcod caught per trawl (1983–90). The locations of the 36 standard stations upon which the lines are based are shown as plus signs. The location of the exceptional 29 May 1990 lingcod catch is marked with a star.



Cobb midwater trawl equipped with a 0.945 cm ($\frac{3}{8}$ inch) stretched-mesh inner liner. Depending on bottom depth, the net was towed horizontally with the headrope at 6 or 32 m below the water's surface for 15 minutes at a speed of 1.0 knot. Survey methods have been described in detail elsewhere (Wyllie Echeverria *et al.*, 1990).

To determine the overall spatial pattern of lingcod within the study region, the abundance of lingcod from all trawls, excluding one large and exceptional catch, was spatially contoured by kriging. Patchiness was measured using the negative binomial coefficient $\kappa$ (Jahn and Smith, 1987).

A series of 20 conductivity–temperature–depth (CTD) casts were made in a grid centered over the location of the exceptional lingcod catch. These casts were all completed within 24 h of the time the trawl was conducted and constituted a routine part of survey procedures (e.g. Schwing *et al.*, 1990). All CTD data were collected with a Sea-Bird Electronics SEACAT-SBE-19 profiler cast to maximum depths of 500 m. The CTD data were analysed by spatially contouring the density of water ($\sigma_t$) over a series of depths, particularly at 10 m (approximate depth of the tow).

In the laboratory, the SL of each fish was measured and sagittal otoliths were removed from 63 specimens that spanned the full size distribution of fish caught. Otoliths were processed following methods described in Laidig *et al.* (1991).

To supplement these samples, lingcod larvae were collected along the central California coast between Point Reyes and Cypress Point from 10 to 15 February 1991. Specimens were collected with a 1 m bongo net (505 $\mu$m mesh) using standard CalCOFI protocols (Smith and Richardson, 1977). Plankton samples were placed in 80% ethanol and larvae were later sorted in the laboratory where otoliths were removed.

Counts of daily increments in the otolith were initiated at the first dark check mark that both completely encircled the primordium and was subsequently enveloped by complete rings of smaller width. The otolith radius (OR) at this mark was 28.6 $\mu$m ($\pm$ 1.6 $\mu$m), which agreed well with a prediction of the size of the otolith at hatch (32.0 $\mu$m) produced from a regression of OR on SL and known size at hatch (7 mm SL; Giorgi, 1981).

The age and SL data were modeled with a four-parameter growth equation (Schnute, 1981). From the initial estimates, the model was simplified to the three-parameter Gompertz growth function. The log-transformed version of the equation was fitted owing to heteroscedastic variance (Zweifel and Lasker, 1976), i.e.

$$\log_e [SL] = \log_e [l_0] + \mathrm{k}(1 - e^{-gt}) \qquad (1)$$

where $l_0$ is length at birth, k is instantaneous rate of growth, $g$ is the rate of decrease of k, and $t$ is age (days). Using Giorgi's (1981) estimate of size at hatch, the intercept term in the final fit was fixed at $l_0 = 7.0$ mm. The inverse of the fitted growth model was used to predict the age of each lingcod taken in the trawl. The distribution of hatching dates was then calculated by subtracting each predicted age from the date of capture.

## RESULTS

Pelagic juvenile lingcod were most abundant in the Gulf of the Farallones and showed a strong nearshore distribution (Fig. 1). Contour plots showed mean abundances of 5.0 lingcod per trawl at depths less than 50 m in the Gulf of the Farallones, decreasing to 1.0 per trawl in deeper waters. Pelagic juveniles were not taken off the continental shelf, i.e. deeper than 183 m (100 fathom contour).

Juvenile lingcod have a very patchy distribution ($\kappa = 0.03$). This low value of $\kappa$ is influenced greatly by one exceptional catch of 230 fish made on 29 May 1990 at

04:15 just offshore of Point Reyes, California (location marked in Fig. 1). This one sample represented 0.148% of the 678 trawls conducted from 1983 to 1990, but accounted for 29.7% of all lingcod captured. The 230 fish from this trawl compare with an overall mean of 0.97 lingcod/trawl (SE = 0.23) taken in the remaining 677 trawls. Moreover, the fish demonstrated a wide size range, from a minimum of 25.7 mm SL to a maximum of 77.1 mm SL. The size distribution peaked between 50 and 60 mm, and was slightly skewed toward larger fish.

The fit of the log-transformed Gompertz equation to the age data was good (Fig. 2; $F_{0.05} = 49778.0$, d.f. = 2,63; $r^2 = 0.854$). Parameter estimates were $\hat{k} = 3.669 \pm 0.316$ and $\hat{g} = 0.0124 \pm 0.0016$ day$^{-1}$. Although not used in fitting the model, we have included in the figure the age data from four larvae sampled in 1991. The proximity of the data to the regression line suggests that the juvenile equation may also apply to larval lingcod.

The estimated hatch date distribution of fish from the large sample peaked around 24 March and ranged from 10 March to 19 April (Fig. 3). The distribution had a wide spread of hatch dates; the extremes ranged over 40 days, indicating that the lingcod in the catch did not come from one egg mass.

A geostrophic interpretation of the density field ($\sigma_t$) at several depths offshore of Point Reyes suggests that an anticyclonic eddy existed south-west of the site of the large lingcod catch (Fig. 4). Clockwise circulation of this eddy would transport water coastally and create a nearshore region of diminished stagnant flow. Anticyclonic flow immediately north of Point Reyes has been observed during the upwelling season (Schwing *et al.*, 1990). The area is directly inshore of a persistent streamer of cold upwelled water that moves south along the coast of northern California and offshore at Point Reyes (Schwing *et al.*, 1991). Water trapped near the coast off Tomales Point contrasts with strong southerly flow offshore.

**Figure 2.** Predicted length (SL) from the log-transformed Gompertz equation as a function of age in days (solid curve). The open circles are lengths versus age data used in the model fit. The filled squares are data from four larvae sampled in 1991, which were not included in the fit.

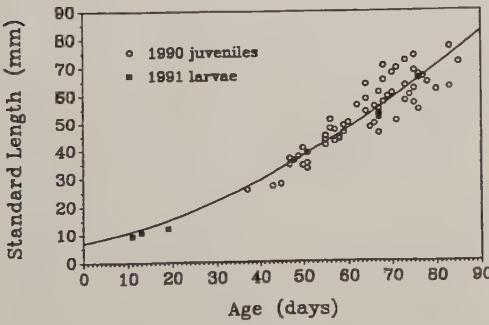
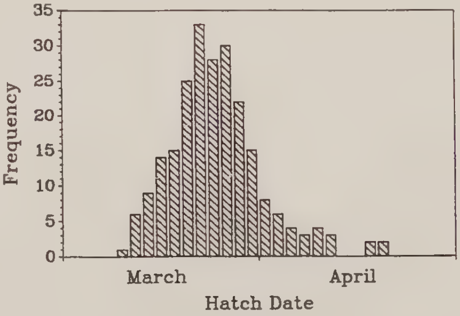


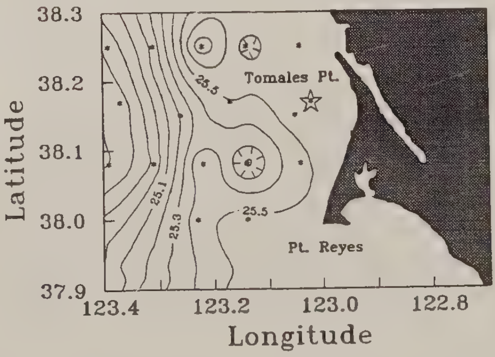
**Figure 3.** Frequency distribution of hatch dates for 230 juvenile lingcod taken in the 29 May 1990 sample.



## DISCUSSION

The data presented here indicate that lingcod off central California hatch during March and April, grow rapidly, and are patchily distributed nearshore as juveniles. Hatching during March and April implies a January–February spawning season for lingcod, assuming that 7 weeks represents the length of the demersal egg stage (Cass *et al.*, 1990). These findings are consistent with reported spawning dates of mid-January to mid-

**Figure 4.** Spatial contouring of the density of water ($\sigma_t$) at 10 m depth from a series of 20 CTD casts made on 28–29 May 1990. The location of the large lingcod catch is marked with a star. Seventeen of the 20 CTD locations are shown as asterisks; the remaining three occurred just west of the figure.



February and hatch dates of mid-March to April for lingcod in British Columbia (Cass *et al.*, 1990).

Lingcod growth during the pelagic juvenile stage is rapid; fish reach 70 mm SL in 80 days. Also, the Gompertz growth model provided a good fit and it may be possible to extend it to other years, because the ages and lengths of four larval fishes caught in 1991 (Fig. 2) lay close to the regression.

Pelagic juvenile lingcod are distributed in a very patchy manner. The estimated negative binomial coefficient ($\hat{k} = 0.03$) is quite low for pelagic early life history stages, which are typically $< 0.4$ (Jahn and Smith, 1987). Adult groundfish values usually range from 0.1 to 1.0 (Lenarz and Adams, 1980).

Beyond suggesting an association with the eddy, we cannot provide an explanation for the occurrence of this unusual catch. The convergent effect of the eddy may have been due to either physical or biological mechanisms. For example, passive drifters transported south in the persistent offshore current could be shunted to the stagnant water near the coast where they could accumulate. A biological explanation is that the eddy somehow resulted in conditions favorable to the survival of juvenile lingcod. Either explanation is consistent with the observed wide distribution of hatch dates.

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# OCEANIC FACTORS INFLUENCING DISTRIBUTION OF YOUNG ROCKFISH (*SEBASTES*) IN CENTRAL CALIFORNIA: A PREDATOR'S PERSPECTIVE

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## ABSTRACT

We used the diet of a seabird, the common murre (*Uria aalge*), to assess the abundance of juvenile rockfish (*Sebastes* spp., mostly *S. jordani*) in the Gulf of the Farallones, California, 1973–90. On the basis of an exploratory analysis of the data and of several oceanographic factors, we hypothesize that availability of fish in the study area during June–July was a function of advection during the January–February period of rockfish parturition. When upwelling or downwelling was persistent in winter, there were few juveniles in late spring, but when upwelling had been mild or pulsed, juveniles were abundant. Rockfish availability also decreased when turbulence, sea level, and sea-surface temperature were high during winter. Stepwise multiple regression analyses indicated that, among these variables, advective transport significantly affects the distribution of juvenile rockfish.

## RESUMEN

Usamos la dieta del ave marina alca piquilarga (*Uria aalge*) para estimar la abundancia de rocot juveniles (*Sebastes* spp., principalmente *S. jordani*) en el Golfo de Farallones, California, 1973–90. Basándonos en un análisis exploratorio de los datos así como en factores oceanográficos, presentamos la hipótesis que la disponibilidad de peces en Junio–Julio fué función de la advección durante Enero–Febrero (la temporada de cría los rocot). Cuando hubo surgencias o hundimientos de masas de agua persistentes en invierno, disminuyó la abundancia de juveniles en primavera tardía, mientras que cuando las surgencias fueron poco intensas u ocurrieron intermitentemente, la abundancia de los juveniles incrementó. La disponibilidad de los rocot disminuyó cuando en invierno hubo valores altos de turbulencia, nivel del mar o temperatura superficial. Análisis de regresión múltiple por pasos indicaron que de entre ésas variables, la advección afecta significativamente la distribución de rocot juveniles.

## INTRODUCTION

Eastern boundary currents contribute roughly a third of the world's fishery resources (Thompson 1981). Such productivity is attributable, in part, to the dominant oceanographic feature of these areas — upwelling of cold, nutrient-rich waters to the surface, which in turn leads to enhanced phytoplankton growth. Parrish and MacCall (1978) examined the relations between several environmental variables and the recruitment success of Pacific mackerel (*Scomber japonicus*) in southern California, and found the highest correlation with the upwelling index (Bakun 1973) at 30°N during the early part of the spawning season. The correlation was positive, and Parrish and MacCall stated that "upwelling is obviously related to recruitment, because it determines the basic productivity of the California Current."

Associated with upwelling, however, is wind-generated turbulence, which could lead to impaired nutrient and carbon transfer to higher trophic levels. For example, Peterman and Bradford (1987) found a negative linear relationship between the mortality rate of northern anchovy (*Engraulis mordax*) during the first 15 days of the larval period and a measure inversely related to turbulence, i.e., the number of periods of calm at 33°N during the main spawning season. Neither cannibalism, as measured by the biomass of adults, nor advection, as measured by offshore Ekman transport, improved the explanation of variability in early mortality. Further, as noted by Methot (1983), even though advection may not have increased mortality during the first 15 days of the larval period, it may have reduced the proportion of larvae that remain in favorable habitat, thereby contributing to late mortality.

Bailey and Francis (1985) found strong year classes of Pacific whiting (*Merluccius productus*) only when sea-surface temperature (SST) in the Los Angeles Bight was relatively high, and when upwelling at 36°N was relatively low at the beginning of the spawning season. They showed that whiting larvae are found farther offshore and to the south in cold years and in years of relatively high upwelling. They concluded that this could be either because spawning takes place farther offshore and to the south or

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[Manuscript received April 1991.]

because of advection. They cited evidence that the larvae grow more slowly during cold years and that prey densities are relatively low offshore and to the south.

Fishery oceanographers have long believed that advection could be an important factor in the reproductive success and recruitment of fish. Bakun (1986) and Simpson (1987) discuss some of the physical mechanisms involved in advection and some physical phenomena that would retain eggs and larvae in favorable habitat.

In order to deter the offshore transport of larvae, fishes in eastern boundary currents tend to reproduce when advection (Ekman transport) is low. They also tend to bear their young alive; relatively large larvae are more capable of swimming than, for instance, newly hatched northern anchovies (Parrish et al. 1981). We found that prevalence of the young-of-the-year (YOY) of one genus of live-bearing fish, *Sebastes*, varies from year to year in the diet of an apex predator, the common murre (*Uria aalge*), in California (Ainley and Boekelheide 1990). To determine what factors might explain the availability of rockfish, we analyzed the relations between several oceanographic factors and the prevalence of rockfish in the murre diet.

## METHODS

A seabird, the common murre, was our fish-sampling tool. We studied murre diet at Southeast Farallon Island (SEFI), 42 km offshore of central California (figure 1), each June and July for 18 years, 1973–90. Murres carry fish in their beaks, in full view, to feed their offspring. From within a blind that overlooked a group of approximately 100 pairs of breeding murres within 10 m of the blind, we observed birds returning from the sea with fish (Ainley and Boekelheide 1990). Observations were made every 3 to 5 days throughout the chick-rearing season, from late May to early July. Using 8 × binoculars (for a "frame-filling" view of each murre), we identified, to the closest taxon possible, 800 to 4000 prey items per year (Ainley and Boekelheide 1990). Years when sample sizes were smaller were oceanographically anomalous years, such as during El Niño events, when fewer pairs were breeding (Ainley and Boekelheide 1990).

We used the proportion of juvenile rockfish in the diet as an index to rockfish availability within the foraging range of the murres. Murres' preferred prey were juvenile rockfish (Ainley and Boekelheide 1990). When rockfish were not available, the murres fed along the mainland coast on other species of fish, principally anchovies. Murres dive to a depth of about 100 m, which corresponds to the depth of the continental shelf in the study area. They forage up to 80 km from breeding sites. Thus, allowing for the shape of the mainland coastline and the fact that it lies only about 40 km from SEFI, the murre population can sample about 7000 km$^2$ of ocean during the summer breeding season, including the entire volume of water overlying the continental shelf and upper slope.

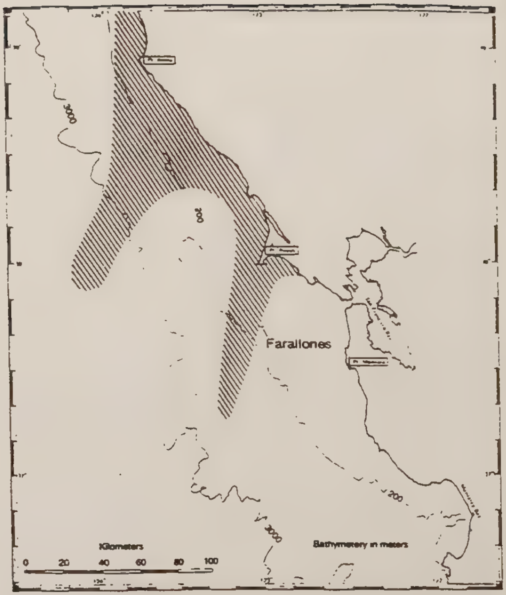

Figure 1. Upwelling plumes of a size and shape typical of early spring in central California, and the location of the Gulf of the Farallones study area (shape of the plume drawn according to figure 4.2.2-27 in SAIC 1987).

During June 1985 and 1986, we collected 24 and 42 common murres, respectively, at various locations within the study area. Gut contents analysis revealed 274 juvenile rockfish in the 1985 sample, and 87 in the 1986 sample (PRBO unpubl. data), and many rockfish were fresh enough to identify to species. These data provided a check for the identifications made at SEFI.

From 1983 to 1991, the National Marine Fisheries Service, Tiburon Laboratory (NMFS), estimated the abundance and distribution of juvenile rockfish in waters off central California, including those surrounding the Farallon Islands (our murres were collected on these cruises). The more classical research method used by NMFS—a grid of trawl stations during late May and June (Wyllie Echeverria et al. 1990; Adams 1992)—overlapped the time of our observations at SEFI. The proportion of juvenile rockfish in the murre diet (as a measure of annual variability in the abundance of the fish) correlated with the NMFS trawl data during overlapping years when trawl results were consistently derived from year to year (1986–91, including 1991 to increase the sample size); a regression between murre diet and log-transformed trawl results for fishes in the size classes appropriate to murre foraging (>39 mm; see Results) was highly significant ($R^2 = 0.87$, $t = 5.27$, $P < 0.01$; figure 2). Therefore, we believe that the bird diet serves as a valid index to the availability of juvenile rockfish in the Gulf of the Farallones region during early summer. We use the diet data for comparison with oceanographic conditions because this time series is much longer than that of the trawl data.

We related the proportion of rockfish in the murre diet to indices of upwelling ($m^3/sec^{-1}/100\ m^{-1}$ of coastline; Bakun 1973) and turbulence (wind speed$^3$), SST, and sea level. We used the upwelling index as a surrogate measure of Ekman transport (advection). Monthly upwelling indices were taken from Bakun (1973), Mason and Bakun (1986), and unpublished updates. A turbulence index consisting of monthly wind-speed-cubed values was derived from 6-hr wind-speed values that were inferred by Bakun from atmospheric pressure fields supplied by the U.S. Navy's Fleet Numerical Oceanography Center. A preliminary analysis with these data indicated that the upwelling index and turbulence estimates derived for 36°N are more representative of conditions in the study area than those at 39°N (F. Schwing, Pacific Fisheries Environmental Group, NMFS, Monterey, pers. comm.). At SEFI we measured SST daily. We used sea level measured at San Francisco (units in mm) as an index to the strength of northerly flow in the California Current and an integration of temperature by depth and region—factors known to affect the marine climate of eastern boundary currents (Norton et al. 1985). Finally, we related rockfish values to measures of wind pulsation, defined as the number of wind events (velocity >9 kts terminated by winds <9 kts) per month. At SEFI we measured winds daily at 0800 PST.

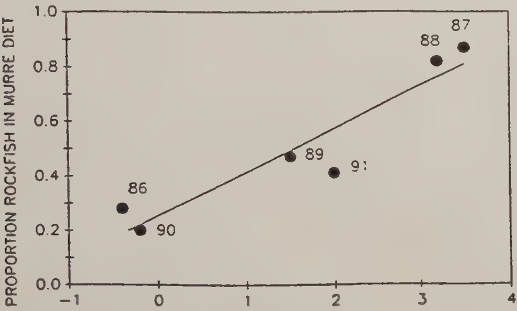

Figure 2. The relation between the proportion of the murre diet contributed by rockfish and the log of the number of juvenile rockfish (>39 mm) in NMFS trawl samples, 1983–91. The relation is described by the equation, $Y = 0.272 + 0.165X$.

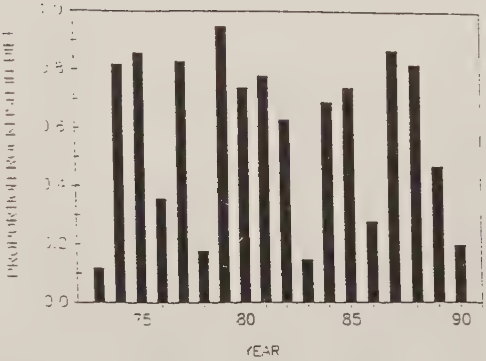

Figure 3. Annual variability in the proportion of rockfish in the diet of the common murre, Southeast Farallon Island, June and July 1973–90.

We correlated the percentage of rockfish in the birds' diet with the above oceanographic and meteorological values averaged for individual and combined monthly periods, October to June, preceding the June–July chick-feeding period. Initially, we used simple regression analyses to investigate relations among these variables; we also tested for correlations among the measures. We used quadratic values of upwelling, turbulence, and SST to model apparent curvilinear relations. To examine the relative effect of each oceanographic variable on rockfish availability, we used forward and backward stepwise multiple regression. Statistical significance was assumed if nominal $P < 0.05$. We recognized that the large number of tests increases the probability of failing to reject false hypotheses, and thus consider this an exploratory analysis.

## RESULTS

Rockfish in the common murre diet varied substantially from one year to the next (figure 3). Regression analyses of rockfish in the diet against the upwelling index, turbulence, SST, and sea level indicated which values provided significant correlations (figure 4). The average January-plus-February upwelling index ($UJ+F$) related to rockfish availability in a parabolic fashion (figure 5) and explained 61% of the variation in interannual abundance ($Y = 79.54 + 1.51\,(UJ+F) - 0.11\,((UJ+F)^2)$; separately, neither month was significantly related to rockfish abundance. Rockfish were most available when the

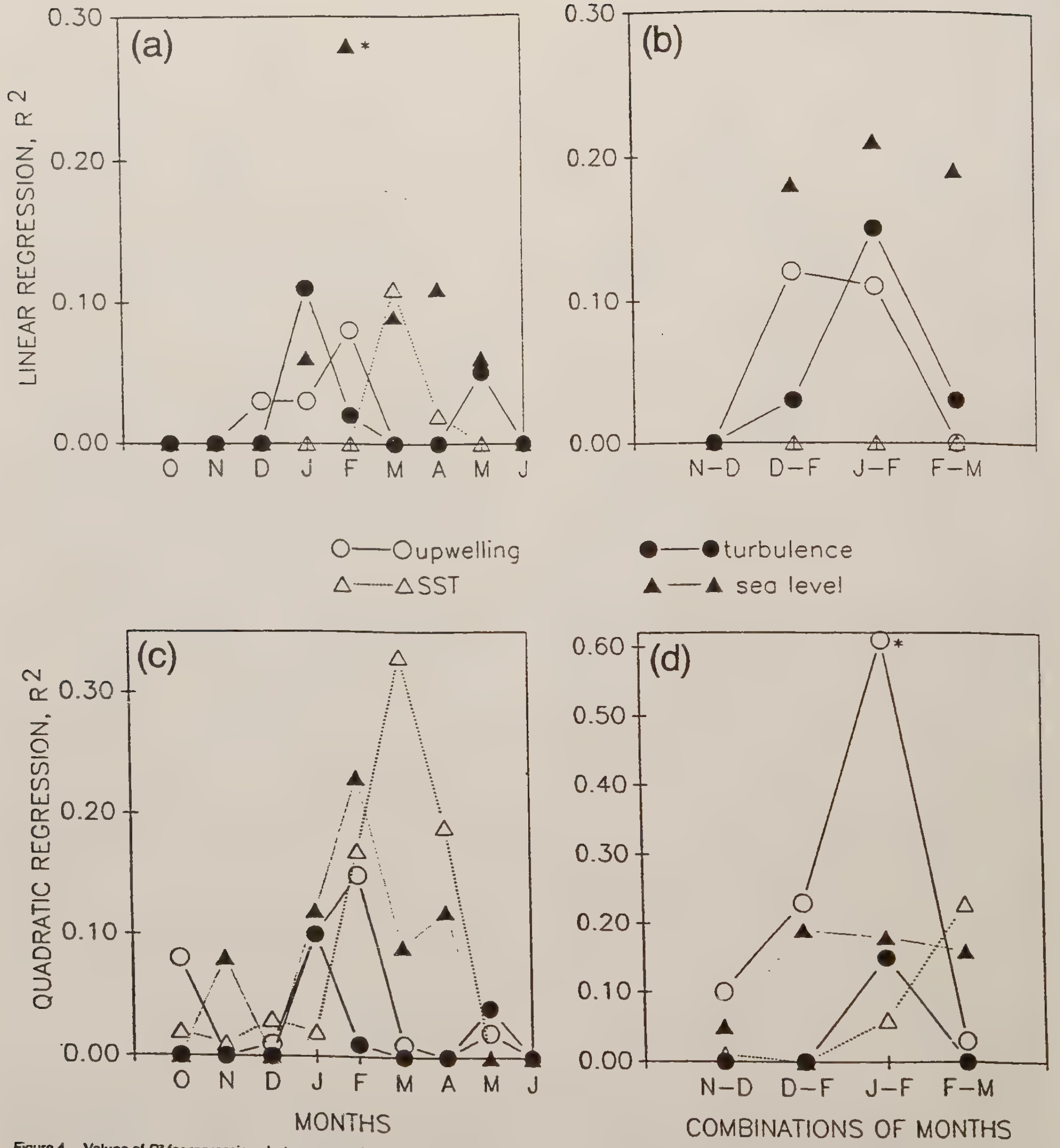

Figure 4. Values of $R^2$ for regressions between prevalence of rockfish in the murre diet and four oceanographic parameters: *a*, linear regression by month, and *b*, by combinations of months; *c*, quadratic regression by month, and *d*, by combinations of months. Significant values are indicated by an asterisk (*).

average January–February upwelling index was slightly above zero. During years of prevalent winter downwelling (1973, 1978, 1983, and 1986), or years when winter upwelling was overly persistent (1976, 1989, 1990), rockfish were less abundant (figure 3; see also Ainley and Boekelheide 1990). We found no significant relations between rockfish abundance and monthly upwelling indices later in the spring and summer, when upwelling reaches its maximum intensity in the California Current sys-

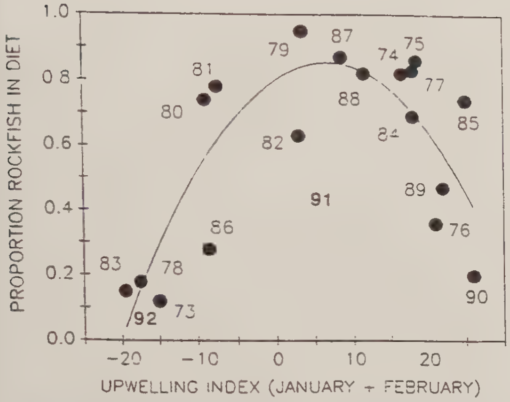

Figure 5. Parabolic relation between rockfish in the diet of murres in the Gulf of the Farallones during June and July and the upwelling index during the preceding January and February, 1973–90. The relation is described by the equation $Y = 79.54 + 1.51(UJ + F) - 0.11((UJ + F)^2)$.

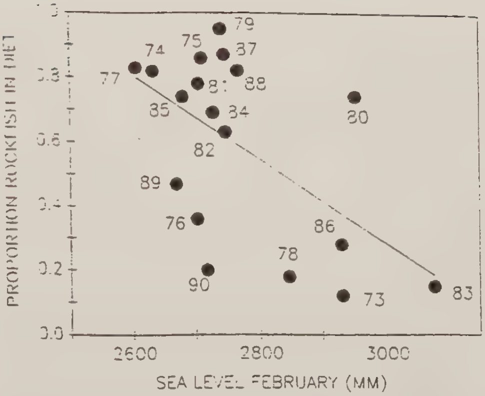

Figure 6. The relation between rockfish in the diet of murres in the Gulf of the Farallones during June and July and sea level during the preceding February, 1973–90.

tem (Breaker et al. 1983). Neither did we find any relation with wind pulsation.

Rockfish availability was negatively, but not significantly, correlated with turbulence during January–February (figure 4; $P = 0.0635$). This variable accounted for only 15% of the yearly variation in fish prevalence. Again, separate turbulence values for January or February were even more weakly related to rockfish availability. Turbulence was greatest during 1978, 1980, 1983, and 1986; the winters of 1978, 1983, and 1986 were also characterized by intense downwelling and elevated sea level. We detected no departure from linearity ($P > 0.10$) between turbulence and rockfish availability.

In March, SST was negatively, but weakly, correlated with rockfish abundance. The quadratic of March SST accounted for 33% of the variation in annual rockfish prevalence, but was again not significant (figure 4; $P = 0.052$). The warmest March SSTs were noted in 1978, 1983, and 1986.

Sea level during February was negatively and significantly correlated with rockfish prevalence (figures 4 and 6; $P = 0.014$), when it accounted for 28% of the yearly variation in rockfish abundance. Sea level was highest in 1973, 1978, 1980, 1983, and 1986. Although sea level in 1976, 1989, and 1990 was low, rockfish were scarce. A linear relation was more significant and explained more of the variance than did a quadratic relation.

The January–February upwelling index, March SST, February sea level, and January–February turbulence values correlated significantly (table 1). The upwelling index was negatively correlated with SST, sea level, and turbulence. SST was positively correlated with sea level and turbulence, and sea level and turbulence also were positively associated. Forward multiple regression indicated that January–February turbulence ($F = 0.10$), March SST ($F = 0.25$), and February sea level ($F = 0.80$) were insignificant when January–February upwelling was first entered into the model. A backward regression analysis confirmed these findings (table 2). The explan-

TABLE 1

**Correlation Coefficients among Four Environmental Factors in Central California, 1973–90**

| | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| 1. Upwelling, Jan.–Feb. | 1.000 | | | |
| 2. Temperature, Mar. | −0.8416 | 1.000 | | |
| 3. Sea level, Feb. | −0.8192 | 0.7455 | 1.000 | |
| 4. Turbulence, Jan.–Feb. | −0.7736 | 0.6823 | 0.7964 | 1.000 |

Each value alone had significant or nearly significant correlation to the prevalence of rockfish in the diet of murres at the Farallon Islands.

TABLE 2

**Backward Regression of January + February Upwelling Index (UI), February Sea Level (SL), and March Sea-Surface Temperature (SST) with Rockfish Prevalence in the Murre Diet**

| Model | $R^2$ | $F$ | $P$ |
|---|---|---|---|
| UI, UI$^2$, SST, SL | 0.58 | 6.81 | 0.0035 |
| UI, UI$^2$, SST | 0.59 | 9.17 | 0.0013 |
| UI, UI$^2$, SL | 0.60 | 9.50 | 0.0011 |
| UI, UI$^2$ | 0.61 | 14.03 | 0.0004 |
| SL, SST | 0.23 | 3.55 | 0.0547 |
| UI | 0.11 | 3.11 | 0.0971 |
| SL | 0.28 | 7.54 | 0.0144 |
| SST | 0.11 | 3.08 | 0.0986 |

$R^2$ values were adjusted by the degrees of freedom and sample size ($n$ = 18 years).

atory power of the model was greatest when only the upwelling index was included. SST and sea level contributed little to explaining variation in rockfish prevalence in the diet and could be dropped from the model with no effect on $R^2$ values.

## DISCUSSION

Most of the rockfish eaten by murres at Southeast Farallon are YOY shortbelly rockfish (*S. jordani*) — on average, 70% of rockfish in the summer diet (Ainley and Boekelheide 1990). This species has also dominated midwater trawl catches of YOY rockfish in the study area (Wyllie Echeverria et al. 1990; Adams 1992), as well as the fish contained in murre stomachs during the two years of collections (Briggs et al. 1987; Ainley, unpublished data). The shortbelly constitutes the largest biomass of any rockfish off California and is a species of the continental shelf and upper slope (Pearson et al. 1991). January and February are the peak months of parturition for this and most other abundant rockfish species that inhabit offshore central California (Wyllie Echeverria 1987), and are the months just before the spring transition from winter conditions to the upwelling period (Breaker et al. 1983). Murres begin to feed on these fish, along with other prey of the same size, as soon as the prey appear in winter (PRBO unpublished data). By the time the rockfish have increased from about 1 cm to 4 cm they are big enough to be carried to chicks at SEFI breeding sites.

The correlation with the upwelling index indicates to us that intense and persistent midwinter winds, either onshore (negative upwelling) or offshore (positive upwelling), transport larvae and perhaps small juveniles away from the foraging range of murres at the Farallones. It is at this time, just after birth and when they are smallest, that YOY rockfish are most vulnerable to advection. Figure 1 depicts an upwelling plume typical of this coast during the early upwelling period (March–April; see also figure 3 in Parrish et al. 1981). Later (June), when upwelling is intense and continuous, plumes in this area of the coast are much broader and extend much farther offshore (SAIC 1987). Along this coast, murres tend to feed at the periphery of upwelling plumes, because there are no prey in recently upwelled water (Briggs et al. 1988). On the basis of this pattern and our analysis herein, we conjecture that large, intense plumes may completely displace YOY rockfish from the foraging range of Farallon-based murres. Advection outside of the murre foraging range — i.e., away from the continental slope (the main habitat of shortbelly and certain other rockfish) — may remove young rockfish from the population unless they can compensate by swimming, or survive until fortuitous currents carry them back to suitable habitat. Whether or not such advection strongly affects recruitment of rockfish, however, remains to be determined (and is being investigated by NMFS). Hobson and Howard (1989) reported mass mortality of YOY shortbelly rockfish on the California shore, not the usual shortbelly habitat (and certainly outside of murre foraging habitat), and conjectured that they had been transported in waters propelled by intense shoreward winds.

Upwelling has the potential to increase primary production in coastal waters of eastern boundary currents, as well as to decrease the egg and larval survival of spawning pelagic fishes because of turbulence and advection (Bakun 1990; Cury and Roy 1989). Our analysis indicates that increased transport of young (larval and small) juvenile fish away from traditional areas for recruitment is an important factor. We base our hypothesis — "The observed pattern of presence or absence of fish is explained by advection" — partly upon the reasoning of Cury and Roy (1989): fish (in this case, rockfish) should bear their young within the central upwelling area of the California Current just before the seasonal onset of intense upwelling. By eliminating the passive (planktonic) egg and reducing the early larval stage, they should be better able to cope with turbulence and advection, which are also caused by the intense, upwelling winds that are the nemesis of smaller developmental stages of the fish. Indeed, by bearing their young alive, rockfish eliminate about 40 days' free existence in the passive stages. This idea assumes that incubation time would be the same as gestation time if rockfish spawned eggs rather than bearing viable larvae. If it is assumed that incubation time of (hypothetical) egg-laying rockfish would be similar to that of other egg layers, then only about one week of passive drifting would be eliminated.

On the other hand, many rockfish species apparently bear their young when they do in order to avoid the intense offshore transport characterizing late spring in the California Current region, as well as perhaps to take advantage of spring plankton blooms. Through natural selection, the release of rockfish larvae during late winter may have evolved because upwelling events are usually intermittent at that time. Upwelling events that are mild or short lead to an enhanced food web. Resulting upwelling plumes may displace the fish slightly offshore, but the young fish are able to return because, between the upwelling events, slack or onshore winds propel them or allow them to return shoreward. We failed to find a correlation with wind pulsation because years of extended weak transport and intermittent strong winds were those in which YOY rockfish were abundant. In such conditions the swimming ability of the young, but relatively well developed, rockfish larvae is sufficient to accommodate to the food dispersal caused by turbulence.

Our analyses suggest that advection is an important factor determining the occurrence patterns of YOY rockfish in central California. Other factors that perturb the oceanic environment in which these rockfish live also appear to play a role. These factors are represented by SST and sea level in our analyses and, like upwelling, correlated most closely with variability of YOY rockfish during late winter.

## ACKNOWLEDGMENTS

Our work on the Farallon National Wildlife Refuge was made possible through a contractual agreement and the logistic support of the U.S. Fish and Wildlife Service and the National Weather Service, as well as the generosity of the members of and donors to PRBO. PRBO participation in NMFS rockfish cruises was funded during various years by the Environmental Protection Agency, Fish and Wildlife Service, Gulf of the Farallones National Marine Sanctuary, Minerals Management Service, and PRBO itself. Collection of SST at SEFI was accomplished through our participation in a shore-station program managed by the Scripps Institution of Oceanography. Upwelling indices were supplied by D. Husby, Pacific Fisheries Environmental Group, NMFS, Monterey; sea-level data were supplied by G. Mitchum, University of Hawaii. We benefited from discussions of rockfish biology with R. Larson, A. MacCall, S. Ralston, D. Woodbury, and coworkers at the NMFS Tiburon Laboratory. Farallon biologists of PRBO, research personnel at the Tiburon Lab, and the officers and crew of the R/V *David Starr Jordan* aided immensely in the determination of rockfish abundance and murre diet. We thank S. Emslie and A. MacCall for their reviews and constructive comments on this and an earlier version. This is contribution no. 486 of PRBO.

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# *Divergency between average and frontier production technologies: an empirical investigation for Bangladesh*

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Applied economic analysis and policy formation often relies on estimated production technologies. Primal representations of production technologies can be specified as the average production function or as the stochastic frontier. This paper uses nested and non-nested specification tests and assessment of economic variables, including elasticities and marginal products, to evaluate systematic differences between the average production function and three different specifications of the stochastic frontier. Bangladesh serves as an illustrative example. The importance emerges of first beginning any analysis of production technologies with nested hypothesis testing of inefficiency and non-nested hypothesis testing for systematic but unknown differences between the average and stochastic frontier functions followed by nested testing of the final form of the production technology.

## I. INTRODUCTION

In empirical work, the production function is usually estimated by regression analysis and, so, provides only an average relationship between inputs and output, since the regression line is fitted through the mean of the data set. In contrast, the estimation of production frontier corresponds to the formal economic definition of a production function (Tisdell 1982).[1] Applied policy formation based upon estimation of these two alternative representations of the production technology, the 'average' production function (hereafter the production function) and the production frontier, might lead to different policies and conclusions. Hence, an appreciation of the extent of differences of these estimates of the production function can be useful in practice.

The issue of possible differences in the assessment of the production technology by production functions and production frontiers is addressed in this paper. The approach adopted is an empirical one, using a cross-section of data for industries from Bangladesh, to estimate econometrically both an aggregate production function and an aggregate production frontier.[2] The results are used to assess differences in the substitution possibilities between labour and

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[1] For a comprehensive discussion of conceptual issues in the measurement of economic and productive efficiencies see Tisdell (1985).

[2] The current analysis, like the similar analysis of Bairam (1988), does not really identify the (outer) production frontier of the economy, since the output, capital and labour quantities are amalgams. In most industries firms will vary in their technical efficiency, but this is 'concealed' when industry averages are used. Unfortunately, we do not have the data to estimate this 'outer' production frontier for the economy. But it is quite possible, for instance, that employment-generating/displacing effects of new capital when this outer frontier is considered could differ even more substantially from those suggested by the average aggregate production than do the estimates given here for the aggregate production frontier. This suggests that while the type of analysis may give some useful first approximations for policy purposes, that it needs to be supplemented by in-depth studies in industry economics. Furthermore, it may be important to take into account natural resource and sustainability aspects, e.g. role of natural resource stocks in production, before reaching firm policy conclusions from this type of production technology estimation.

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capital, differences in their marginal products, and any final form of the technology found from a series of nested hypothesis tests of constant returns to scale (CRTS) and functional form. Both nested and non-nested specification tests evaluate whether the frontier or production function is more appropriate. It is found that selection between the frontier and production function hinges upon the type of significance tests employed, nested or non-nested, and the initial null hypothesis.

## II. APPROACH AND METHODOLOGY

Technical efficiency and procedures for specification of the production frontier, the functional form, measurement of marginal products and measurement of factor substitution possibilities are discussed in this section.

### *Technical efficiency and production frontiers*

A sector's technical efficiency measures the ability to produce the maximum output possible from a given set of inputs and production technology. Technical efficiency is a relative concept since each sector's production performance is compared with a best-practice input–output relationship. The best-practice performance, or production frontier, is established by the practices of the most efficient sectors. Technical efficiency is then measured as the deviation of the individual sectors from this best-practice frontier.

This best practice is assumed stochastic, with a corresponding two-sided error term, to capture exogenous shocks beyond the control of firms. Since all sectors do not produce the frontier output, an additional one-sided error term is introduced to represent technical inefficiency. This approach contrasts with the production function which provides an average relationship between output and inputs over the entire sample, and in which a single, two-sided error term captures the stochastic influences and unobserved input usage.

The production frontier is estimated by stochastic frontier approach, which may be written (Aigner *et al.*, 1977) as

$$Y_i = h(X_1, X_2, \ldots, X_N, A)\, e^{\Phi_i} \tag{1}$$

where $Y_i$ is the output of the $i$th of the 47 sectors in the Bangladesh economy, $X_j$ is the $j$th of $N$ inputs, $A$ represents a vector of parameters, $e$ is the exponential operator, and $\Phi_i$ is a sector-specific error term. The error term $\Phi_i$ is composed of two independent components: $\Phi_i = V_i - U_i$. The systematic component, $V_i$, represents random variation in output due to factors outside the sector's control (such as weather), measurement error and statistical noise. It allows the deterministic production frontier to be stochastic. The technical efficiency relative to the stochastic frontier, $e^{-U_i} = Y_i/[h(X_1, X_2, \ldots, X_N, A)\, e^{-V_i}]$, is captured by the one-sided error component $U_i \geqslant 0$. When $U_i = 0$, production lies on the stochastic frontier and is technically efficient and, when $U_i > 0$, production lies below the frontier and is technically inefficient.

It is assumed that the symmetric error $V_i$ is independently and identically distributed as $N(0, \sigma_V^2)$ and that the non-negative error $U$ is distributed as the absolute value of a normal distribution, $|N(0, \sigma_U^2)|$, i.e. half-normal, and that $\sigma^2 = \sigma_U^2 + \sigma_V^2$. Define $\delta = \sigma_U/\sigma_V$. The greater $\delta$ is from unity, the more production is dominated by technical inefficiency, while the closer to zero, the more the discrepancy between the observed and frontier output is dominated by random factors beyond the control of the sector.

The inefficient component of $\Phi$ in the stochastic frontier, $U$, might be distributed other than half-normal. One possibility is the exponential distribution. A second possibility, proposed by Stevenson (1980), attempts to add an additional degree of flexibility to the one-sided error distribution. Stevenson proposed a truncated (at zero) normal distribution with non-zero mean for the distribution of $U$. This adds an additional parameter to the model, say $\mu$.

### *Translog production technology*

The production technology was specified as translog, which, following Berndt and Christensen (1973), can be written as

$$\ln Y = \alpha + \alpha_K \ln K + \alpha_L \ln L + \alpha_{KK} \ln K \ln K + \alpha_{KL} \ln K \ln L + \alpha_{LL} \ln L \ln L \tag{2}$$

where $Y$ represents output, $K$ is capital, and $L$ is labour. The translog production technology was interpreted as a second-order approximation to an underlying, unknown technology rather than as a direct representation of technology.

### *Marginal products*

Marginal products can be derived from the translog form. The logarithmic marginal product for capital may be written as

$$\delta \ln Y/\delta \ln K = (\delta Y/\delta K)/(K/Y) = \alpha_K + \alpha_{KK} \ln K + \alpha_{KL} \ln L.$$

Rearranging yields:

$$\delta Y/\delta K = [\alpha_K + \alpha_{KK} \ln K + \alpha_{KL} \ln L][K/Y].$$

Similarly, $\delta Y/\delta L = [\alpha_L + \alpha_{KL} \ln K + \alpha_{LL} \ln L][L/Y]$. A production function is usually considered to be well-behaved only if output increases monotonically with all inputs. Monotonicity holds if $\delta Y/\delta K > 0$ and $\delta Y/\delta L > 0$.

### *Elasticities of substitution*

From the translog production technology (Equation 2), one can compute the elasticity of substitution between inputs. Substitution elasticities are measured using Hicks' elasticity of complementarity (HEC) rather than the widely applied

Allen elasticity of substitution (AES) because of biases introduced in the latter when derived from a translog production function (Field 1988).[3] The cross HEC may be written as

$$h_{ij}=(\alpha_{ij}+M_iM_j)\ /M_iM_j \tag{3}$$

where $M_i$ is the logarithmic marginal product of factor $i$, $\ln(\delta Y/\delta X_i)$ . A positive (negative) value of $h_{ij}$ indicates that inputs $i$ and $j$ are $q$-complements ($q$-substitutes), so that increased usage of one increases (decreases) the usage of the other. With the Cobb–Douglas form, $\alpha_{ij}=0$ and $h_{ij}=1$.

The own HEC may be written as

$$h_{ii}=(\alpha_{ii}+M_i^2-M_i)\ /M_i^2 \tag{4}$$

Own HECs should be negative. Unlike the AESs, any maintained separability restrictions are directly imposed.

The HECs or AESs do not provide direct information on the behaviour of relative factor shares, but the direct elasticity of substitution (DES) and Morishima elasticity of substitution (MES) do (Sato and Koizumi, 1973; Blackorby and Russell, 1989; Kang and Brown, 1981). Because computation of the MES from the translog technology faces the same computational bias as the AES, attention has been restricted to the DES.

The DES measures the substitution between two inputs along an isoquant with all other inputs and output held constant. Following McFadden (1963), the DES between $X_i$ and $X_j$ is defined as

$$d_{ij}=[\mathrm{d}(X_i/X_j)/\mathrm{d}(f_i/f_j)][(X_i/X_j)/(f_i/f_j)] \tag{5}$$

where $f_i=\delta f(X)/\delta X_i$ and $i$ is not equal to $j$. The DES is a generalization of the two-factor elasticity of substitution formula applied to each pair and is symmetric. The DES lies between zero and infinity, and grows larger as the substitution becomes easier between two inputs. The DES is a two-factor, two-price elasticity of substitution. The DES is a short-run elasticity since it holds all other inputs constant, but under weak (or strong) separability (or only two inputs), the DES, a short-run measure, equals the long-run two-factor, two-price elasticity of substitution for the separable inputs (Mundlak, 1968).[4]

The DES for the translog production technology at the point of approximation may be written as (Boisvert, 1982)

$$d_{KL}=\frac{-[\alpha_K+\alpha_L]}{-[\alpha_K+\alpha_L]+\dfrac{\alpha_K^2\alpha_{LL}-2\alpha_K\alpha_L\alpha_{KL}+\alpha_L^2\alpha_{LL}}{\alpha_K\alpha_L}} \tag{8}$$

## III. ESTIMATION

In comparison to the maximum likelihood estimates of the frontier model, 'Ordinary least-squares estimates are inefficient and the estimate of the constant term is inconsistent (at least within the assumptions of the frontier model)' (Greene, 1990, p. 329). The differences between the average production function and the frontier should be intercept differences (Cowing *et al.*, 1988). This can be seen from $V_i$ in the frontier error term $V_i-U_i$. In the average function this would be absorbed in the constant term, shifting it neutrally downward, leaving the slope coefficients the same. However, the slope coefficients might also display statistically significant differences since the OLS estimates are inefficient (Greene, 1990).

However, as noted by Cowing *et al.* (1988), the statistical and the economic differences (e.g. elasticities, scale economies, marginal products) must be distinguished. In their own words, 'Even if frontier estimates are statistically different from the OLS estimates, it may be the case that such differences are of little economic importance. This question is of interest, for, ..., frontier estimation is considerably more difficult than least squares' (Cowing *et al.*, 1988, p. 65).

### *Model specification*

An industry-level production technology was estimated for 47 sectors of the Bangladesh economy during 1976–77.[5] The output $Y$ was defined as the sectoral outputs in millions of Taka. Two inputs per sector were specified: $K$ for capital in millions of Taka and $L$ for labour in thousands of man-years. As discussed above, the stochastic production frontier has an additive two-sided error term normally distributed and representing random disturbances. The other component represents deviations in technical efficiency. Three alternative specifications are evaluated: (1) half-normal (2) exponential and (3) the generalized form of Stevenson (1980). The production function is estimated with a single additive, normally distributed error term, which represents stochastic disturbances.

### *Nested hypothesis testing and final form of the technology*

The general translog form of the production technology in Equation 2 might not be the final form, which in turn has important implications for the elasticities of substitution, marginal products, and measures of economies of scale.

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[3] Field (1988) notes that AESs estimated from the (primal) translog production function may not be desirable because the matrix of the estimated coefficients must be inverted to derive an AES. If one coefficient has a large standard error, all AESs are affected.

[4] Hence, the results for the separable inputs hold for both partial and full static equilibrium and any output level. In addition, the (symmetric) DES provides information on the relative shares of inputs $i$ and $j$, $S_i$ and $S_j$, where sign is $\delta(S_i/S_j)\ /\delta(X_i/X_j)\ >|=|<0$ according as $d_{ij}>|=|<1$ (Sato and Kazomi, 1973). Thus, if capital $K$ is substituted for labour $L$, so that the ratio of capital to labour increases, the share of capital increases/remains constant/decreases relative to the share of labour as $d_{KL}>|=|<1$.

[5] The existence of an aggregate production technology is assumed, which in turn requires the maintained hypothesis of additive separability among firms (van Daal and Merkies, 1984).

Restrictions on the production possibilities can be tested by a series of nested econometric restrictions on the production technology, Equation 2. The translog production technology might be characterized by CRTS or even the more restrictive Cobb–Douglas form. In the latter case, the technology is globally homogeneous, strongly separable in the inputs, and with constant unitary elasticities of substitution. In contrast, the technology with the translog form is not restricted to homogeneity and the elasticities of substitution are not *a priori* restricted constant or strongly separable in the inputs.

These hypothesis tests follow a nested sequential procedure, starting with a test for constant returns to scale and proceeding to tests for the Cobb–Douglas form and Cobb–Douglas with CRTS. Each succeeding hypothesis is tested given that the previous hypothesis is maintained. The testing procedure ends whenever a hypothesis is rejected. Following Denny and Fuss (1977), the overall significance of the nested hypothesis tests is approximately the sum of the individual test's significance. A significance of 0.025 is assigned for each test, giving an overall significance of 0.075. Because the translog function is interpreted as a second-order approximation to an underlying production technology, the tests hold only at the point of approximation and approximately in the neighbourhood of the point of expansion (Denny and Fuss, 1977).

CRTS requires the following econometric restrictions on the translog production function of Equation 2 (Berndt and Christensen, 1973):

$$\alpha_K+\alpha_L=1 \quad \text{and} \quad \alpha_{KK}+\alpha_{LL}+\alpha_{KL}=0 \tag{7}$$

The restriction for the Cobb–Douglas functional form is

$$\alpha_{KL}=0 \tag{8}$$

If the null hypothesis (Equation 8) is not rejected, homogeneity, strong separability and unitary elasticities of substitution among all inputs are maintained hypotheses. The restriction for constant returns to scale with Cobb–Douglas is (given $\alpha_{KL}=0$)

$$\alpha_K+\alpha_L=1 \tag{9}$$

### *The data*

The data used in this paper are taken from Alauddin (1986) and Alauddin and Tisdell (1988) and the 47-sector input–output table prepared by the Bangladesh Planning Commission (BPC, 1980a, b). The details of the sector classification scheme, the methodology of estimates and their limitations have been discussed elsewhere by Alauddin (1986) and Alauddin and Tisdell (1988) so we do not wish to repeat them here. Estimates of capital requirements were obtained by taking the product of the fixed capital coefficients for various industries and their corresponding output levels as reported by the Bangladesh Planning Commission (BPC 1980a, pp. 12–24). Depending on the sectors, these coefficients were estimated on three different bases, the details of which appear in BPC (1980a, p. 24). Clearly, the estimates involve conjectures and may not be entirely reliable and, therefore, they may have serious limitations for policy purposes. It is well-known that many conceptual difficulties and statistical pitfalls surround the estimation of capital stock (see, for example, Harcourt, 1973). Nevertheless, given that the primary objective of the paper is to illustrate how there can be a divergence between average and frontier production technology estimates using the same data base, the accuracy of the data estimates can be considered to be of secondary importance.

Note that the data, since they relate to the year 1976–77, are quite old. Although a 53-sector input–output table for a later year, 1981–82, is available (BPC, 1990), the employment series for that particular year is not yet available. The 1981–82 data could not be used for this analysis. Fortunately, the 1976–77 data still enable the main methodological issues to be investigated empirically.

### *Econometric estimation*

Econometric estimation of the frontier form of the translog production technology given in Equation 2 used maximum likelihood under the behavioural assumption of the expected profit maximization for the three distributions of $U_i$.[6] Symmetry of the second-order coefficients follows from Young's theorem on the order of differentiation of a continuous function, and the symmetry is imposed as a maintained hypothesis in Equation 2, giving: $\alpha_{KL}=\alpha_{LK}$.

Estimation of the standard translog production function given in Equation 2 was by OLS under the hypothesis of the expected profit maximization. The $R^2$ was 0.855, indicating a good fit for the cross-sectional data. The Lagrange multiplier test of Breusch and Pagan (1979) for a null hypothesis of heteroscedasticity of the form Var $[\varepsilon]=h(\beta'X)$ gave a chi-square test statistic of 6.422 with five degrees of freedom, thereby not rejecting the null hypothesis at the conventional levels of significance.[7] As a consequence, White's (White,

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[6] Zellner *et al.* (1966) showed that a direct estimation of the primal production technology without this behavioural assumption gives biased and inconsistent estimates because of simultaneity between inputs and output. Under the behavioural assumption of the expected profit maximization, inputs may be assumed exogenous rather than endogenous.

[7] Interpreting the production technology as a second-order approximation, rather than as a direct representation, of technology and use of an additive error term introduces heteroscedasticity because the remainder term of the second-order Taylor series approximation is incorporated into the residuals (Kulatilaka, 1987). In addition, the use of data aggregated by arithmetic means can also introduce heteroscedasticity. Heteroscedasticity is also often found in cross-sectional data. Hence, a very general form of heteroscedasticity from a number of sources is allowed .

Table 1. *Nested hypothesis tests for final form of production technology*

| | Chi-square or $F$-test | | | |
|---|---|---|---|---|
| | Stochastic production frontier | | | |
| Hypothesis test | Half-normal | Exponential | Generalized | Production function |
| CRTS translog | 193.225 (2) | 194.340 (2) | 144.877 (2) | 1.2941 (2,41) |
| Cobb–Douglas functional form | | | | 4.402 (3,41) |
| CRTS Cobb–Douglas form | | | | 206.60 (1,44) |

Note: Wald test for production frontier and $F$-test for production function. Level of significance for each individual test is 0.025 and overall significance is 0.075. Degrees of freedom in parenthesis.

1980) procedure was applied to obtain heteroscedastic-consistent estimates of the parameters.[8]

A direct estimation of the production technology, under the hypothesis of the expected profit maximization, was elected rather than the estimation of the production technology and its first-order conditions (less one), since the latter approach requires constant returns to scale for the cost shares to sum to unity and thereby avoid singularity of the variance–covariance matrix of residuals. Moreover, estimation of Equation 2 with its first-order conditions without scaling of the data by sample means (to maintain consistency between the production frontier and production function) places the residuals from the objective function and the first-order conditions on the same measurement scale. Finally, estimation with cross-sectional, rather than time-series, data and with the small number of explanatory variables should minimize any multicollinearity that might arise from the direct estimation rather than the systems approach of Equation 2 and its first-order condition.[9]

### *Final form of the production technology*

The results of the nested hypothesis testing for the final form of the production technology for the production frontiers and production function are summarized in Table 1. The overall level of significance for each nested testing sequence was 0.075, while the level of significance for each test within each nested testing sequence was 0.025. The three production frontiers are considered first and then the production function. Wald tests (Godfrey, 1988) were used for the production frontiers and $F$-tests were used for the production function. The Wald test is distributed as chi-square with degrees of freedom equal to the number of independent restrictions.

The Wald test rejected the null hypothesis of constant returns to scale in all the specifications of the stochastic frontier. Because the testing is nested, it was terminated at this point. In sum, the unrestricted translog frontier was not rejected at an overall level of significance of 0.075 (and lower) as the final form of the frontier. The parameter estimates are reported in Table 2.

The null hypothesis of CRTS for the translog production function was not rejected at both the 0.025 and 0.01 levels of significance, since the $F$-statistic was $F(2, 41) = 1.2941$, with numerator and denominator degrees of freedom in parenthesis. The null hypothesis of Cobb–Douglas functional form for the production function was rejected at a 0.025 level of significance by an $F$-test with $F(3, 41) = 4.402$, but was marginally rejected at 0.01 significance. The null hypothesis of CRTS for the Cobb–Douglas production function was rejected. The Breusch–Pagan test for heteroscedasticity gave a chi-square test statistic with two degrees of freedom of 47.2501, decidedly rejecting the null hypothesis of no heteroscedasticity. The estimates were corrected for heteroscedasticity (heteroscedastic-consistent estimates), following White (1980).

## IV. COMPARISON OF PRODUCTION TECHNOLOGY

The nested hypothesis tests for the final forms of the stochastic production frontiers and production function indicated that, at the 0.075 level of overall significance, both representations of production possibilities were translog, with the production function displaying CRTS. Moreover, there was an indication that, at a lower level of overall significance, the final form of the production function would be Cobb–Douglas.

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[8] Heteroscedasticity of the production *frontier* cannot be tested by the Breusch–Pagan test and corrected with current econometric packages. Hence, it is not known if the frontier's parameter estimates are heteroscedastic or not and the parameter estimates of the *frontier* function are not necessarily heteroscedastic-consistent.

[9] The condition index detects multicollinearity and is the square root of the ratio of the largest to the smallest characteristic root of $X'X$, where $X$ is the vector of regressors (Belsley *et al.*, 1980). The computed value of 0.0159 indicates that multicollinearity does not pose a serious problem.

Table 2. *Parameter estimates of production technology*

| | Production function | | | Stochastic frontier | | |
|---|---|---|---|---|---|---|
| Variable | Cobb–Douglas | Unrestricted translog | CRTS translog | Half-normal | Exponential | Generalized likelihood |
| Intercept | 3.793* | 1.989* | 2.776* | 2.317* | 2.147* | 2.261 |
| | (0.868) | (0.391) | (0.146) | (0.682) | (0.685) | (13.804) |
| Capital | 0.271* | 0.817* | 0.868* | 0.826* | 0.822* | 0.817* |
| | (0.111) | (0.195) | (0.185) | (0.260) | (0.258) | (0.300) |
| Labour | 0.443* | 0.572* | 0.132* | 0.559 | 0.565 | 0.572 |
| | (0.095) | (0.219) | (0.185) | (0.325) | (0.323) | (0.373) |
| Capital squared | | −0.027* | −0.035 | −0.027 | −0.027 | −0.027 |
| | | (0.024) | (0.027) | (0.033) | (0.033) | (0.038) |
| Labour squared | | 0.065 | 0.111* | 0.067* | 0.066* | 0.065* |
| | | (0.030) | (0.018) | (0.018) | (0.018) | (0.020) |
| Capital* labour | | −0.082* | −0.076 | −0.082 | −0.082 | −0.082 |
| | | (0.036) | (0.039) | (0.047) | (0.047) | (0.054) |
| $\sigma^2=\sigma_U^2+\sigma_V^2$ | | | | 0.394* | 0.541* | 0.662 |
| | | | | (0.123) | (0.165) | (7.365) |
| $\mu$ | | | | | | 0.0002 |
| | | | | | | (63.259) |
| Log-likelihood | | | | −39.919 | −39.893 | −40.111 |

Note: Translog functional form unless otherwise stated. Standard errors in parentheses. Heteroscedastic-consistent estimates for standard production function.
*Denotes significance at 5% level.

### *Statistical tests for equality of coefficients*

A direct comparison of parameter estimates for the translog production function and the stochastic production frontier reported in Table 2 indicates fairly close similarity between the intercepts and first-order and second-order coefficients.[10]

As discussed above, the differences between the stochastic production frontier and the production function should be intercept differences, so that the stochastic frontiers and production function merely represent neutral shifts from one another. The slope coefficients, however, might display statistically significant differences due to the inefficient estimates of OLS. Following Cowing *et al.* (1988), statistical tests of these differences were conducted. An $F$-test on the null hypothesis that all coefficients except the intercept are the same in the stochastic frontiers was first run against both the unrestricted and CRTS translog production functions as the null. The estimated $F$ for the unrestricted (CRTS) translog production function as the null was: (1) $F(5,41)=0.2043$ (3.836), for the half-normal; (2) $F(5,41)=0.2040$ (3.938) for the exponential; and (3) $F(5,41)=0.5639$ (3.813) for the generalized likelihood, indicating no statistically significant difference. The null hypothesis that all intercept coefficients were the same in both models was tested by a Wald test with the stochastic frontier as the null. The chi-square statistic of the Wald test with five independent restrictions for the unrestricted (CRTS) translog production function gave a value of: (1) 23.0505 (467.402) for the half-normal; (2) 23.005 (470.848) for the exponential; and (3) 0.042598 (456.161) for the generalized likelihood, rejecting the null hypothesis for the half-normal and exponential forms but not for the generalized likelihood with the unrestricted translog production function and uniform rejection for the CRTS translog production function.

The second-order coefficients play a crucial role in flexible functional forms, giving them their 'flexibility'. Test of significance for the null hypothesis of no differences in the second-order coefficients against the unrestricted (CRTS) translog production function as the null gave: (1) $F(3,41)=0.0002$ (2.905) for the half-normal; (2) $F(3,41)=0.0003$ (2.980) for the exponential; and (3) $F(3,41)=0.0002$ (3.058) for the generalized likelihood, all implying no differences for the unrestricted translog but differences for the CRTS translog. The Wald test of no differences in the second-order coefficients against the stochastic frontier as the null gave chi-squares with three degrees of freedom for the unrestricted (CRTS) translog of: (1) 269.165 (14.903); (2) 399.00 (15.456) and (3) 292.008 (14.142), respectively, for the half-normal, the exponential and the generalized likelihood, rejecting the null hypothesis of no differences for both the unrestricted and CRTS translog production function.

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[10] We may have omitted variable bias in the estimated coefficients, since land and human capital, the omitted variables, are likely to be correlated with the included variables.

Table 3. *Hicks elasticities of complementarity*

| | Production function | | | Stochastic frontier | | |
|---|---|---|---|---|---|---|
| Variable | Cobb–Douglas | Unrestricted translog | CRTS translog | Half-normal | Exponential | Generalized likelihood |
| Capital | −2.696 | −0.264 | −0.196 | −0.250 | −0.257 | −0.264 |
| Labour | −1.258 | −0.549 | −0.207 | −0.630 | −0.563 | −0.550 |
| Capital–labour | 1 | 0.825 | 0.337 | 0.822 | 0.823 | 0.825 |

Note: Calculated at point of approximation.

Table 4. *Direct elasticities of substitution*

| | Production function | | | Stochastic frontier | | |
|---|---|---|---|---|---|---|
| Variable | Cobb–Douglas | Unrestricted translog | CRTS translog | Half-normal | Exponential | Generalized likelihood |
| Capital–labour | 1.000 | 1.207 | 8.078 | 1.294 | 1.211 | 1.207 |

Note: Calculated at point of approximation.

In sum, mixed information was found on the statistical differences between the coefficients of the production function and the three stochastic frontiers.

### *Economic differences*

Since parameter estimates from second-order functional forms, whether interpreted as direct or second-order approximations of technology, have little meaning in themselves, the factor substitution possibilities, marginal products and scale economies are examined next in order to make more meaningful comparisons about the production technology and implications for economic policy formation. The elasticities were evaluated at the point of approximation.

The Hicks elasticities of complementarity (HEC) for the translog form are reported in Table 3. The HECs are negative for both the production frontiers and the production function, as expected for a well-behaved production technology. The own HECs are inelastic for both the production frontiers and translog production function, with the production function having slightly larger absolute values for own HECs. The HECs for the CRTS translog production function were more inelastic than the unrestricted translog or Cobb–Douglas forms. The HECs between capital and labour indicated inelastic *q*-complementarity, so that increased usage of one increases the demand or marginal product of the other. Complementarity among inputs, or 'cooperant' factors, is generally expected to prevail (Hicks, 1946; Sakai, 1974). Policy formation based upon an accurate measurement of the cross HEC should give similar results (unless the production function is interpreted as Cobb–Douglas, where $\mathrm{HEC}_{KL}=1$).

The direct elasticities of substitution (DES) for capital and labour are reported in Table 4. The DESs for the production frontier and the production function are all around 1.207, except for the CRTS translog production function, which has a DES of 8.078. Hence, the capital–labour isoquants for the production frontiers and unrestricted translog production function are similar and are more elastic and flatter in shape than that for the Cobb–Douglas form and the CRTS translog production function's DES is considerably more elastic than any other. Moreover, if capital $K$ is substituted for labour $L$, so that the ratio of capital to labour increases, the share of capital will increase relative to the share of labour for both the production frontiers and function if the latter is interpreted as translog. If the production function is Cobb–Douglas, then the income shares are constant. In sum, policy targeting income distribution and relative factor shares could provide very dissimilar results, depending upon the specification of technology.

The marginal products for the production frontiers and the production function are reported in Table 5. They are calculated for mean values of capital, labour and output. They are all positive, indicating that the monotonicity condition of a well-behaved production technology is satisfied. In this case, marginal products for the production frontiers and the production function are virtually the same. Hence, policies requiring knowledge of marginal products, such as those targeting allocative efficiency, would provide virtually identical results.

Economies of scale can be measured as the sum of the production coefficients: $\delta \ln Y/\delta \ln K+\delta \ln Y/\delta \ln L$. At the point of approximation, this measure becomes simply $\alpha_K+\alpha_L$. This value is 1.386, 1.388 and 1.389, respectively, for the half-normal, exponential and generalized production

Table 5. *Marginal products*

| | Production function | | | Stochastic frontier | | |
|---|---|---|---|---|---|---|
| Variable | Cobb–Douglas | Unrestricted translog | CRTS translog | Half-normal | Exponential | Generalized likelihood |
| Capital | 0.355 | 1.126 | 1.196 | 1.138 | 1.133 | 1.126 |
| Labour | 0.027 | 0.056 | 0.013 | 0.057 | 0.858 | 0.058 |

Note: Calculated at point of approximation.

frontiers, is 1.389 and 1.000 for the unrestricted and CRTS translog production functions, respectively, and 0.714 for the Cobb–Douglas. Hence, economic policies targeting scale economies would be affected by the specification of the production technology.

### *Fitted values*

The fitted values from the translog stochastic frontiers and the translog production function should match one another if the two give equivalent representations of technology. The fitted values were regressed from the unrestricted translog production function upon those of the stochastic frontier with the half-normal error term in the relationship $Y=\alpha+\beta X$ to evaluate slope intercept differences between the two series. Ideally, the intercept should be zero and the slope unity if the two data series are the same. The results of the regressions were:

| | coefficient | $t$-ratio |
|---|---|---|
| $\alpha$ | $-0.0179$ | $-2.060$ |
| $\beta$ | 1.0024 | 723.549 |

with $R^2=0.999941$. The intercept $\alpha$ clearly differs from zero given the $t$-ratio of $-2.060$. This result is expected if the intercepts between the translog stochastic frontiers and production function are different due to the technical inefficiency term $U_i$ in the stochastic frontier's disturbance term. The $F$-test on the linear restriction that the slope is unity, i.e. $\beta=1$, gave the result $F(1, 45)=4.4782$, marginally rejecting the null hypothesis that $\beta=1$ at 0.05 but not at 0.025 or 0.001. In sum, there will be systematic, statistically significant differences between the two due to the disturbance term, affecting the intercepts, and possibly the slope coefficients.

### *Nested and non-nested tests*

The relationship between the unrestricted translog stochastic frontiers and unrestricted translog production function can be tested formally. The production function can be viewed as a restricted version of the stochastic frontier through the error term $\Phi_i=V_i-U_i$. The econometric restriction is $\delta=\sigma_u/\sigma_v=1$. Hence, as inefficiency becomes insignificantly small, the frontiers' probability density functions become indistinguishable from the normal for $U_i$ distributed half-normal, exponential or following the generalized likelihood. The estimated values of $\delta$ are: (1) $\delta=0.646$ with a standard error of 2.242 for the half-normal; (2) $\delta=0.5977$ with a standard error of 5.784 for the generalized likelihood; and (3) $\delta=6.196$ with a standard error of 20.312 for the exponential. The results indicate that there are no statistical differences between the different translog stochastic frontiers and unrestricted translog production function estimated by OLS.

The test on $\delta$ and on the equality of coefficients specifies the alternative to the null and contains the null as a special case. Hence, this is a nested specification test. When the alternative is fully specified but does not contain the null model as a special case, specification tests are known as non-nested or encompassing hypotheses (Godfrey, 1988).

These non-nested tests can be applied to the translog stochastic frontier and the unrestricted translog production function as a check that a systematic but unknown difference does not exist. The MacKinnon et al. extension (MacKinnon *et al.*, 1983) of the $J$-test (Davidson and MacKinnon, 1981) was applied. The $t$-ratio for the test against the stochastic frontier as the null was 0.606 and the log-likelihood was $-39.826$. The $t$-ratio for the test against the unrestricted translog production function as the null was $-0.340$ and the log-likelihood was $-39.816$. The results lend weight to the conclusion that there are no statistical differences between the two unrestricted translog models.

## V. CONCLUDING REMARKS

It has been shown that depending on the method of hypothesis testing and the initial null hypotheses chosen, significant differences or no differences between the estimated average production function and the stochastic production frontier and various functional forms may be observed. Because of these the following procedures are suggested.

It may be preferable to first begin any analysis of production technologies with nested hypothesis testing of technical inefficiency and non-nested hypothesis testing for systematic but unknown differences between the unrestricted forms of the average and frontier production functions. Nested specification tests on the final form of the production technology would follow after first selecting between the average and stochastic frontier functions.[11] This hypothesis testing sequence starts from the most general question, that of the average or stochastic frontier representation of technology, and proceeds to specific forms for the selected representation of technology (average or frontier). While this sequence is not formally and explicitly nested, it does proceed from the most general to the most specific.[12] Alternatively, beginning hypothesis testing for the final form of the technology could give misleading results without first testing between the average and stochastic frontier functions. In turn, economic policy formation, such as that based on relative income shares, factor substitution possibilities, and technical efficiency differentials could differ.

For the Bangladesh data, nested hypothesis tests on the final form of the production technology indicated a significant difference between the average production function and stochastic production frontier; the average production function was CRTS translog and possibly even Cobb–Douglas and all three stochastic frontiers were unrestricted translog. In contrast, nested hypothesis tests of technical inefficiency and non-nested hypothesis testing for systematic but unknown differences indicated no significant differences. Certainly, for the Bangladesh data we examined, economic policy could have built inappropriately upon a translog stochastic production frontier rather than the appropriate CRTS translog or perhaps Cobb–Douglas average production function. In this case, there is little scope for policies to improve management efficiency by ensuring that all sectors adopt frontier management practices, since these practices are already being adopted and deviations are due to random factors.

The frequency of divergent results, such as those obtained on the basis of the Bangladesh data, is difficult to anticipate *a priori*. Instead, it seems to be an empirical issue, which must be examined on a case-by-case basis.

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[11] Selection of the average production function and estimation by OLS would not imply inefficient estimates in comparison to the frontier model, since that inefficiency is predicated on a distinguishable difference between the two models.

[12] The tests of technology and pooling would not be nested as a group. Hence, the statistical significance of the tests would not be the (approximate) sum of the individual tests' significances (cf. Denny and Fuss, 1977). However, Godfrey (1988) notes that when there is a high degree of dependence between the individual significance tests, the actual overall significance level may be somewhat smaller than its upper bound of $s\alpha$, where $s$ is the number of tests and $\alpha$ is the significance level of each test.

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# Testosterone response to a gonadotrophin-releasing hormone agonist in Hawaiian monk seals (*Monachus schauinslandi*)

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Adult male Hawaiian monk seals were administered a gonadotrophin-releasing hormone (GnRH) agonist to determine its effectiveness in reducing the testicular production of testosterone. Blood samples were collected from four treated seals and two control seals at weekly intervals for 10 weeks and again at the beginning of the following breeding season. The GnRH-agonist had an initial, brief, stimulating effect on circulating testosterone, but this was followed by an inhibitory effect that lasted for 7 to 8 weeks. The plasma concentrations of testosterone were within normal ranges by the following spring. These results demonstrate a reversible form of long-term androgen suppression, which may have applicability in a variety of wildlife management programmes.

## Introduction

The Hawaiian monk seal (*Monachus schauinslandi*) was listed as 'endangered' in 1976 after a 50% reduction in the number of seals observed in beach counts over 20 years (Johnson *et al.*, 1982). In addition to the reduction in the number of animals, three of five major breeding populations also showed an imbalance in the adult sex ratio. Although the cause and chronological development of this condition remain uncertain, by the early 1980s, when extensive monitoring of the population began, male Hawaiian monk seals outnumbered females by at least 2:1 at Laysan Island (Johnson and Johnson, 1981), Lisianski Island (Stone, 1984) and Kure Atoll (Gilmartin, *et al.*, 1986). The disparate sex ratio at Kure Atoll was resolved by management actions which included introducing females and enhancing survival of young females (Gerrodette and Gilmartin, 1990; Van Toorenburg *et al.*, in press).

The skewed adult sex ratio still exists at Laysan and Lisianski Islands and it is associated with anomalous breeding behaviour termed 'mobbing'. Mobbings are mass matings wherein groups of males (4–14 or more) attempt copulation with a female or with an immature seal of either sex. Mobbing events have been observed to last several hours and usually result in severe injury and often death of the adult female or immature seal, either directly from the injury or indirectly by shark attack (Johnson and Johnson, 1981; Johanos and Kam, 1986; Alcorn and Buelna, 1989). The differential mortality between the adult sexes owing to mobbing attacks appears to be a major factor in maintaining these skewed sex ratios in adults and perpetuating mobbing incidents.

The Hawaiian monk seal is a seasonal breeder (Kenyon and Rice, 1959; Atkinson and Gilmartin, 1992) and mobbing attacks by adult males occur during the height of the breeding season, from May to July (L. M. Hiruki and W. G. Gilmartin, unpublished), when most females have weaned their pups and are thought to be resuming ovarian activity. This period correlates with the annual peak in circulating testosterone in males (Atkinson and Gilmartin, 1992).

Gonadotrophin-releasing hormone (GnRH) agonists have been used in humans to suppress secretion of testicular androgen to reduce the probability of metastasis of androgen-dependent prostate carcinomas (Parmar *et al.*, 1985). Similarly, GnRH agonists have been shown to suppress androgen production in dogs (Sandow *et al.*, 1980), monkeys (Sundaram *et al.*, 1982) and rodents (Redding *et al.*, 1984), with an attendant decrease of libido in dogs (Sandow *et al.*, 1980). However, reduction of testosterone production alone, via castration, does not always reduce androgen-mediated behaviour in dogs (Le Boeuf, 1970). In the harbour seal (*Phoca vitulina*) testosterone reduction by GnRH agonist has been shown to correlate with a reduction in sociosexual behaviour (Yochem *et al.*, 1991). Thus, we hypothesized that treatment of Hawaiian monk seals with a GnRH agonist would suppress testicular production of testosterone. The research reported herein was designed to test this hypothesis in captive adult male monk seals and, if an effect was detected, to measure the duration of testosterone suppression.

## Materials and Methods

### *Animals and treatments*

Five captive adult male Hawaiian monk seals, housed at Sea Life Park and Waikiki Aquarium, Oahu, Hawaii, were used for this trial. All of the male seals were at least 10 years old and annual veterinary physical examinations suggested that they

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were in good health. No adult females were present in the enclosures at either site. In June 1990, during the natural breeding season and when secretion of testosterone was at its highest (Atkinson and Gilmartin, 1992), three of the five seals (A, N and P) were given 11.25 mg of a GnRH-agonist, D-Trp6-luteinizing-hormone-releasing hormone (LHRH) (Decapeptyl-CR: Ferring, NY). The dose was determined by multiplying the human dose (3.75 mg) by 3, to approximate an equivalent dose for the seals who weighed about 200 kg. Seals S and Z were not given the drug at this time, but were handled and sampled at the same frequency as the test animals. The GnRH agonist was injected i.m. at three sites in the pelvic area of each of the treated seals. Blood samples were collected before treatment with the agonist and then weekly from all five seals for 10 weeks after the GnRH agonist was administered. The blood sampling procedure has been described (Atkinson and Gilmartin, 1992). Plasma from these samples was stored frozen at −20°C until radioimmunoassay for testosterone could be performed. Four weeks after the first three seals were injected, one of the control seals, animal Z, was given 5.6 mg of the GnRH agonist. Blood sampling for this animal was continued for 8 weeks. Early in the following breeding season, 9 months after the GnRH was given, an additional blood sample was collected from each seal.

### *Hormone measurement*

Testosterone was measured in the plasma with a single antibody radioimmunoassay (Atkinson *et al.*, 1986; Atkinson and Gilmartin, 1992). All oestrogen and progesterone compounds had $< 1\%$ crossreactivity (Atkinson *et al.*, 1986). Crossreactivity with dihydrotestosterone, 4-androstene-3β,17β-diol and androstenedione was 98, 47 and 4.7%, respectively, thus measuring the majority of circulating androgens. Nonspecific binding of the antibody was $< 5\%$, and the sensitivity of the assay was 0.03 ng per tube. Extraction recovery was 88.1%. A pool of monk seal plasma containing $2.06 \pm 0.18$ ng testosterone $\mathrm{ml}^{-1}$ plasma was included in each assay to determine interassay variation, which was $< 15\%$.

### *Statistical analysis*

Log–logit transformations were applied to the standard curve of the assay (Rodbard, 1974). Student's *t* test was used to compare the differences in hormone concentrations before and after injection.

## Results

Two of the three seals, P and N, injected with 11.25 mg GnRH agonist, and seal Z, injected with 5.6 mg, showed transient increases in circulating testosterone 1 week after the injection (Fig. 1). Within 2 weeks of the injections, the plasma concentration of testosterone in all seals had fallen significantly ($P < 0.001$) and remained at similar values to that in castrated animals for 7 to 8 weeks. Between 9 and 10 weeks after the injection, testosterone concentrations in seals A, P and N began to rise (Fig. 1a–c). Testosterone concentrations in seal Z also increased, although the sampling frequency was reduced. The control seal (S) maintained high and relatively constant plasma testosterone concentrations throughout the study (Fig. 1e), while being exposed to the same sampling stress as the experimental protocol. Early in the following breeding season, the mean testosterone concentrations of the treated seals ($0.52 \pm 0.08$ ng $\mathrm{ml}^{-1}$) were similar to that of the control seal (S: 0.60 ng $\mathrm{ml}^{-1}$).

## Discussion

This study demonstrated that an injection of a GnRH agonist can be used to reduce circulating testosterone concentrations of Hawaiian monk seals for about 2 months. The GnRH agonist used in this study (D-Trp6-LHRH) is a potent synthetic LHRH analogue which differs from the naturally occurring LHRH in that the glycine in amino acid position 6 has been replaced by D-tryptophan. This replacement leads to enhancement of the affinity for the LHRH receptors in the pituitary and a longer than normal half-life of the analogue. GnRH agonists initially stimulate the anterior pituitary to produce increased amounts of luteinizing hormone (LH). This was apparent in three of the four seals injected in the present study. While the increase was variable in the animals, we suspect that this was due to the sampling interval and recognize the need to characterize this transient increase with more frequent sampling.

Large doses (Sundaram *et al.*, 1982) or chronic administration of GnRH agonists (Bergquist *et al.*, 1979) have the paradoxical effect of decreasing LH, which leads to a decrease in the production and secretion of gonadal steroids. This decrease in the pituitary response is thought to reflect a desensitization of the pituitary or a refractory phase, accompanied by the down-regulation of local LH receptors (Sundaram *et al.*, 1982). The decreased testosterone is probably due to a decrease in the concentrations of 17,20-desmolase and 17α-hydroxylase in the Leydig cells, leading to a block in the steroidogenic pathway to testosterone synthesis (Chasalow *et al.*, 1979).

All but one dose used in the present study were scaled on a body weight basis from the dose recommended for treatment of male humans with androgen-dependent prostate carcinomas. One seal in the study received 5.6 mg of the GnRH agonist, which is half the dose of the other three treated seals. This half dose resulted in the same reduction in plasma testosterone observed in A, N and P, suggesting that the dose administered to these seals was well above the threshold required to achieve the desired response.

The concentrations of testosterone at the start of the study were similar for all animals except for seal A. Although the testosterone concentration appeared high in seal A, it was within the normal range of captive and wild seals sampled to date (Atkinson and Gilmartin, 1992).

This study was undertaken as a preliminary assessment leading to use of a GnRH agonist as an agent to control aggressive sociosexual behaviour, mobbing, in Hawaiian monk seals in the wild. While the animals in this study were housed in naturalistic enclosures, they were not exposed to adult female monk seals. Thus, it was not possible to assess the effects of the treatment on libido or aggressive behaviour, which exist in the wild during the breeding season when oestrous female seals are available.

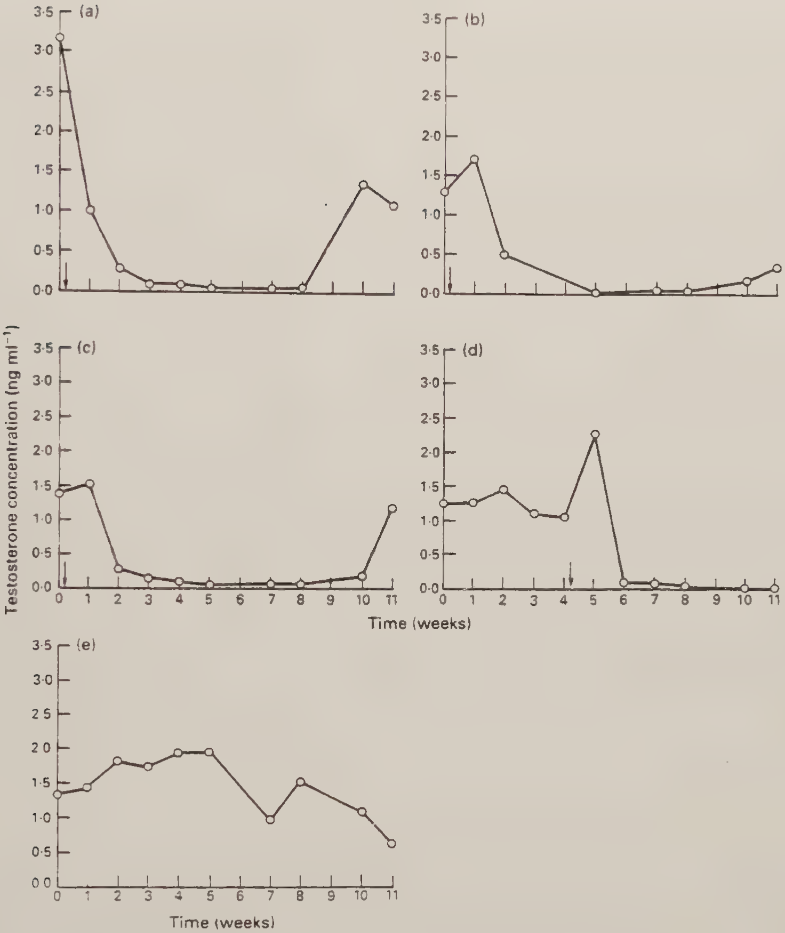

**Fig. 1.** Testosterone concentrations in the plasma of male Hawaiian monk seals injected with D-Trpo-luteinizing-hormone-releasing hormone (LHRH): 11.25 mg for seals (a) A, (b) P and (c) N and (d) 5.6 mg for seal Z. The arrow marks the time of injection. (d) Seal Z served as a control prior to administration of D-Trp6-LHRH at week 4. (e) Seal S served as a control throughout the experiment.

GnRH agonists have various effects on fertility, depending on the species. Dogs (Sandow *et al.*, 1980) appear to be more sensitive to the antigonadal effects of GnRH agonists than are primates (Sundaram *et al.*, 1982) or rats (Chasalow *et al.*, 1979). Sperm production and quality were not measured in the present study; however, the plasma testosterone concentrations of the treated seals did return to the normal breeding season concentrations (Atkinson and Gilmartin, 1992) by the following season, indicating that any effects on fertility were probably reversible. The effects on fertility are an obvious consideration that should be assessed, if restoration of breeding ability is deemed critical, before such treatments are used for behaviour modification in wildlife management programmes.

The GnRH agonist tested, D-Trp6-LHRH, demonstrated the ability to control production of testicular androgen in monk seals for about 2 months. Use of a repeated dose of this agent at 2 month intervals should allow suppression of testosterone for longer periods, increasing the probability that aggressive sexual behaviour in adult male Hawaiian monk seals may be controlled and the number of mobbing attacks reduced.

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# Sulphide tolerance and adaptation in the California killifish, *Fundulus parvipinnis*, a salt marsh resident

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Hydrogen sulphide is a toxicant naturally produced in hypoxic marine sediments, hydrocarbon and brine seeps and hydrothermal vents. The California killifish, a salt marsh resident, is remarkably tolerant of sulphide. The 50% lethal concentration is 700 μM total sulphide in 96 h, and 5 mM in 8 h (determined in flow-through, oxygenated sea water). Killifish exposed to sulphide produce thiosulphate which accumulates in the blood. The cytochrome *c* oxidase (a major site of toxicity) of the killifish is 50% inhibited by $<1$ μM sulphide. Killifish liver mitochondria are poisoned by 50–75 μM sulphide but can oxidize 10–20 μM sulphide to thiosulphate. Sulphide causes sulphhaemoglobin formation (and impairment of oxygen transport) at 1–5 mM *in vitro* and to a small extent at 2 mM *in vivo*. Killifish blood neither catalyses sulphide oxidation significantly nor binds sulphide at environmental (low) sulphide concentrations. Exposure to 200 μM and 700 μM sulphide over several days causes significant increases in lactate concentrations, indicating shift to anaerobic glycolysis. However, individuals with the most lactate die. In terms of diffusible $H_2S$, the killifish can withstand concentrations two to three orders of magnitude greater than would poison cytochrome *c* oxidase. The high sulphide tolerance of the killifish, particularly of concentrations typical of salt marshes, can be explained chiefly by mitochondrial sulphide oxidation. Sulphide tolerance and mitochondrial sulphide oxidation in the killifish have a constitutive basis, i.e. do not diminish in fish held in the laboratory in sulphide-free water for 1–2 months, and are improved by prior acclimation.

Key words: *Fundulus parvipinnis*; sulphide tolerance and detoxication.

## I. INTRODUCTION

Sulphide is an important environmental factor and toxicant for aquatic plants, invertebrates and fishes (Theede *et al.*, 1969; Smith & Oseid, 1974; Ingold & Havill, 1984; Bagarinao & Vetter, 1989; Levitt & Arp, 1991; Bagarinao, 1992). In the marine environment, sulphide is produced mostly from bacterial sulphate reduction in sediments (Fenchel & Riedl, 1970; Jorgensen, 1984). Salt marshes, enclosed bays and estuaries and areas of pollution such as sewage outfalls are characterized by micromolar to millimolar sulphide concentrations in sediments (Bagarinao, 1992, for table of measured values). Effects of sulphide on various enzymes, cellular structures and physiological functions are well documented in the biomedical literature (National Research Council, 1979; Beauchamp *et al.*, 1984; Bagarinao, 1992). The major biochemical lesion caused by sulphide appears to be the inhibition of cytochrome *c* oxidase, the terminal enzyme in the electron transport chain of mitochondria. Another quite colourful effect of

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sulphide is the formation of sulphhaemoglobin, a green derivative with a much reduced affinity for oxygen and therefore non-functional in oxygen transport (Carrico *et al.*, 1978*a*, 1978*b*).

Many species of fish spend all or part of their lives in shallow waters and may experience sulphide. Mass fish kills in dredged or impounded salt marshes, or in earthen culture ponds are often attributed routinely to hypoxia/anoxia, salinity and temperature fluctuations, or low pH (Waggoner & Feldmeth, 1971; Inland Fisheries Project, 1974), but it is quite likely that sulphide is responsible for some fish kills (Torrans & Clemens, 1982). Fishes also occur in the sulphidic water column of the Cariaco Trench (Baird *et al.*, 1973), at the deep-sea hydrothermal vents (Cohen & Haedrich, 1983; Rosenblatt & Cohen, 1986; Cohen *et al.*, 1990; Geistdoerfer, 1991), and hydrocarbon and brine seeps (Brooks *et al.*, 1979; Kennicutt *et al.*, 1985). Yet, sulphide has been almost totally overlooked as an environmental factor for marine fishes, except for our work.

The California killifish, *Fundulus parvipinnis* Girard, is a small, ecologically and physiologically versatile cyprinodontiform that spends its entire life in bays, lagoons and salt marshes from Morro Bay southward to Magdalena Bay in Baja California (Fritz, 1975; Allen, 1982). Earlier comparative studies have shown that the killifish is more tolerant to sulphide than several other species of shallow-water marine fishes (Bagarinao & Vetter, 1989), has remarkable sulphide-oxidizing activity in the mitochondria (Bagarinao & Vetter, 1990), but negligible sulphide-oxidizing and sulphide-binding capacity in the blood under physiological conditions (Bagarinao & Vetter, 1992).

This paper will present a model of sulphide tolerance in the California killifish, based on several sets of data, most of which are presented here, and some already published. The specific questions addressed are:

(i) How much sulphide can the killifish tolerate at the whole-animal level?
(ii) What physiological and biochemical changes occur during exposure to sulphide?
(iii) How much sulphide is inhibitory to killifish cytochrome *c* oxidase?
(iv) What accounts for the high sulphide tolerance of the killifish?
(v) Is anaerobic metabolism an important mechanism in sulphide tolerance?
(vi) Is sulphide tolerance constitutive? Is it improved by acclimation?

## II. MATERIALS AND METHODS

### EXPERIMENTAL ANIMALS

The California killifish used in the experiments consisted of juveniles and adults 50–150 mm in total length and 3–8 g in body weight. They were collected by minnow traps mostly from a creek in the Kendall-Frost salt marsh reserve in the northeast corner of Mission Bay in San Diego, California during winter and spring in 1988–1991.

### SULPHIDE EXPOSURE EXPERIMENTS

The killifish were exposed to sulphide in flow-through aquaria in which sulphide and fully aerated sea water from reservoirs flowed in continuously by peristaltic pumps. Seawater flow rate was 100 ml min$^{-1}$. Stock solutions of sulphide, prepared from thoroughly washed and dried crystals of $Na_2S.9H_2O$ dissolved in nitrogen-bubbled distilled water, was diluted 100-fold in the aquaria. Turnover time for water in the aquaria was 40 min, and oxygen concentrations at the outflows were 50–80% of saturation depending on treatment.

Control fish in the aquarium not receiving sulphide suffered no mortality. Water temperature during the tests was 14–18° C.

Long-term sulphide tolerance was determined by exposure of groups of 10 killifish to different concentrations up to 800 µM sulphide for 96 h. The 96-h $LC_{50}$, the lethal concentration for 50% of the fish was computed by probit analysis. Short-term tolerance was determined by exposure to different concentrations up to 8 mM sulphide for 8 h. In one experiment, 10 California killifish were exposed to each of the following sulphide treatments: 500 µM for 72 h, 1 mM for 8 h, 2 mM for 8 h, and 5 mM until death of 50% of the fish. In a subsequent experiment, duplicate aquaria were stocked with 12 killifish each and exposed to 200 µM, 1 mM, 2 mM, 5 mM and 8 mM sulphide for 8 h. At 2-h intervals, three fish were removed from one aquarium and analysed for haemoglobin spectra, haematocrit, haem concentration, and for sulphide and sulphide oxidation products in the blood (below).

A separate experiment was conducted to see whether killifish shifted to anaerobic metabolism during sulphide exposure. Fish that had been held in the laboratory for 6 months were stocked in the flow-through aquaria in four groups of 25 fish each: (i) fish exposed to 200 µM for 6 days; (ii) fish exposed to 700 µM sulphide for 3 days, and two control groups, one run side by side with each treatment. Fish from treatment and control aquaria were sampled 2 h into the exposure and every day for 6 days in 200 µM, and for 3 days (when all fish died) in 700 µM. During each sampling period, three control and three sulphide-exposed fish were removed, and assayed for blood lactate and enzyme activities in tissue homogenates (below).

Another experiment was made to determine the ' nature/acclimation ' basis of sulphide tolerance in the killifish. Sulphide tolerance may be due to a heritable genetic program (a constitutive basis), or to adjustments individuals make during their lifetimes (an acclimation effect), or to both. The approach taken to determine a constitutive basis was to remove killifish from the salt marsh, keep them in sulphide-free water in the laboratory for a period of months (' de-acclimation ', a term provisionally used for brevity's sake to mean ' acclimation to sulphide-free water in laboratory holding tanks '), and test them for *whole-animal* sulphide tolerance and for *mitochondrial* sulphide oxidation capacity. Conversely, killifish were acclimated in low sulphide (below the previously determined 96-h $LC_{50}$ but probably higher than typical field levels) and tested similarly. Thus, three groups of killifish were exposed to 5 mM sulphide for 8 h: (i) fish newly caught from the salt marsh; (ii) fish de-acclimated for 1·5 months in the laboratory; and (iii) fish acclimated in 200 µM sulphide for 7 days. The control group consisted of newly-caught fish also placed in the aquaria for 8 h but not exposed to 5 mM sulphide. The first two groups were tested with three replicate aquaria with 20 fish each, the third and the control groups with two replicates. After 6–8 h when most sulphide-exposed fish were dying, five dying fish were removed from each group, and blood and other tissues were fixed in monobromobimane and analysed by HPLC (below).

In this paper, ' sulphide ' refers to total dissolved sulphide (the sum of $H_2S$, $HS^-$ and $S^=$), unless otherwise specified. At environmental and physiological pH values, the $HS^-$ anion and the gaseous $H_2S$ forms are the important forms. Uncharged $H_2S$ freely diffuses across membranes, and sulphide toxicity to animals can best be approximated by the $H_2S$ concentration. Thus, the toxic sulphide concentrations will all be recalculated as $H_2S$ in the discussion.

## MEASUREMENT OF BLOOD PARAMETERS

Killifish from the 8-h tolerance tests at different sulphide concentrations were bled via the caudal vein into heparinized microcapillary tubes (length 75 mm, internal diameter 1·15 mm). The tubes were spun for 5 min in an IEC Model MB microhaematocrit centrifuge at 13 460 × *g*, and the haematocrit (packed RBC volume as percent of total blood volume) determined using a reader (microcapillary tubes, centrifuge and reader all from Fisher Scientific). The volume of the packed RBC was calculated to be $\pi r^2 h$ or 1·0387 *h*, where *h* is the height in the capillary tubes. The packed RBC were lysed in 0·2 or 1 ml distilled water and the clear supernatant was scanned for haemoglobin spectra and assayed for haem concentration. Formation of sulphhaemoglobin (SHb) and ferric haemoglobin

($Hb^+$), both indicators of impairment of oxygen transport, was monitored with a Perkin–Elmer Lambda 4A spectrophotometer with software from Softways (San Diego, California) using methods described earlier (Bagarinao & Vetter, 1992). Haem concentration was determined by adding known volumes of haemolysates to 2 ml Drabkin's reagent (Sigma assay kit ♯525), reading the absorbance of the ferric haemoglobin-cyanide derivative at 540 nm after 5 min, and calculating with the extinction coefficient 11 $\text{mM}^{-1}\,\text{cm}^{-1}$.

## CHROMATOGRAPHY OF SULPHUR COMPOUNDS

Sulphide is the most reduced form of sulphur and can be oxidized to elemental sulphur, thiosulphate, sulphite, and/or sulphate depending on the conditions and the organisms involved. The monobromobimane-HPLC method is able to fix and measure sulphide and other reduced sulphur compounds in the same samples (Fahey & Newton, 1987; Vetter *et al.*, 1987, 1989), and has been crucial to our studies of sulphide metabolism by whole animals, mitochondria and blood (Bagarinao & Vetter, 1989, 1990, 1992). During the 8-h tolerance experiments on the killifish, blood, heart/spleen (blood-rich tissues, combined because of small mass) and liver (not as blood-rich) were removed from sulphide-exposed individuals as well as controls and analysed by monobromobimane-HPLC. Various tissues from killifish in the ' nature/acclimation ' experiment were similarly analysed.

## ENZYME ASSAYS

The activities of two key enzymes, cytochrome *c* oxidase (EC 1.9.3.1; ferrocytochrome *c*: oxygen oxidoreductase) and lactate dehydrogenase (LDH; EC 1.1.1.27; $NAD^+$: L-lactate oxidoreductase) were determined spectrophotometrically at 20° C. Tissues of killifish were homogenized in 4 or 9 volumes of 10 mM Tris pH 7·2 and centrifuged for 5 min at 2000 × *g* at 5° C. Each tissue homogenate was assayed in three replicates. For cytochrome *c* oxidase, the 2-ml assay mixture contained 100 mM potassium phosphate pH 6·0, 0·5 mM EDTA and 50 µM reduced cytochrome *c*. Addition of 25 µl of the tissue supernatants initiated the reaction. Activities were calculated from the linear rate of decrease in absorbance at 550 nm within the first 1–2 min, using the extinction coefficient 18·5 $\text{mM}^{-1}\,\text{cm}^{-1}$. Sulphide concentrations inhibitory to cytochrome *c* oxidase in tissue homogenates (*in vitro*) were determined by adding microlitre amounts of sulphide to the assay mixture to achieve final concentrations up to 5 µM. The 50% inhibitory concentration, $IC_{50}$, was estimated by transforming activity data into percent inhibition, plotting them against the logarithm of sulphide concentration and fitting linear regression lines. In addition, inhibition of cytochrome *c* oxidase *in vivo* was monitored during the experiment on anaerobic metabolism.

During the latter experiment, LDH was also assayed in control fish and fish exposed to sulphide for different lengths of time. LDH activity was assayed in 2 ml buffer containing 80 mM imidazole pH 7·0, 200 µM NADH, 5 mM pyruvate and 10 µl tissue homogenate, by following the decrease in absorbance at 340 nm, and calculating with the extinction coefficient 6·22 $\text{mM}^{-1}\,\text{cm}^{-1}$.

## LACTATE ASSAY

Lactate accumulation was used as an indicator of the shift to, and the extent of, anaerobic metabolism in the California killifish during sulphide exposure. Whole blood was obtained by microcapillary tubes and promptly prepared for lactate determination. Samples were transferred into microcentrifuge tubes, diluted with three volumes of ice-cold 6% perchloric acid to precipitate the proteins, and stored frozen until assay at the end of the experiment. Lactate was assayed spectrophotometrically, using Sigma Diagnostics procedure ♯826-UV but scaled down to 750 µl assay volume. The assay mixture contained 197 mM glycine pH 9·2, 164 mM hydrazine, 12·3 units lactate dehydrogenase, 1·85 mM NAD, and 25 µl supernatant of the precipitated blood samples (4 × dilution). The mixture was incubated at 37° C for 30 min, and the absorbance at 340 nm was recorded. Lactate was estimated from the absorbance of NADH, using the extinction coefficient 6·22 $\text{mM}^{-1}\,\text{cm}^{-1}$, and allowing for the dilution of the blood sample. Each blood sample was assayed in three replicates.

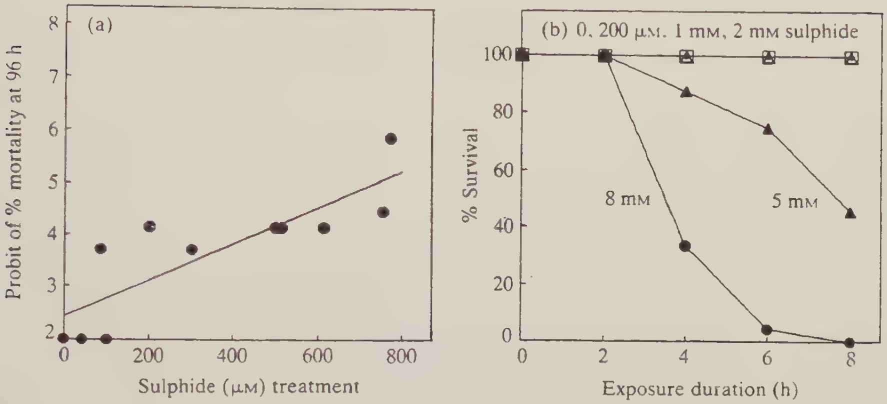

FIG. 1. Tolerance of California killifish to sulphide, determined in a flow-through oxygenated aquarium system. (a) 96-h tolerance; each point is per cent survival among 10 fish. The regression equation is $y=2{\cdot}4+0{\cdot}0037x$, $r^2=0{\cdot}72$, where $y$ is the probit value and $x$ is μM sulphide. (b) Tolerance of fish exposed to high sulphide concentrations for up to 8 h; each point is the average survival in two aquaria with 12 fish each.

## ASSAY OF SULPHIDE OXIDATION CAPACITY OF MITOCHONDRIA

Killifish mitochondria have previously been shown to rapidly oxidize low micromolar concentrations of sulphide exclusively to thiosulphate, a reaction that is stoichiometrically and obligately linked to oxygen consumption (Bagarinao & Vetter, 1990). Mitochondrial oxygen consumption in the presence of sulphide is therefore a direct measure of the sulphide oxidation capacity of killifish mitochondria. To determine whether mitochondrial sulphide oxidation was constitutive and/or improved by prior acclimation, mitochondria were isolated from five groups of killifish and assayed for oxygen consumption in the presence of sulphide. The five groups consisted of 40 fish each: (i) newly caught; (ii) de-acclimated for 1 month; (iii) de-acclimated for 2 months; (iv) acclimated to 200 μM sulphide for 10–12 days (with 20% mortality); and (v) acclimated to 500 μM sulphide for 10–12 days (with 50% mortality). Three mitochondrial preparations were made on three consecutive days from each group, each preparation from the livers of 10 killifish (seven fish for group 5). Each mitochondrial preparation was assayed three times in the presence of 3 mM succinate (a control substrate) and 10, 20, 50 and 75 μM sulphide according to methods described by Bagarinao & Vetter (1990).

## STATISTICAL ANALYSIS

Analysis of variance (ANOVA) and related tests were done by hand according to Zar (1984), and probit analysis with the BMDP computer program.

# III. RESULTS

## SULPHIDE TOLERANCE OF WHOLE FISH

Mortality after 96-h exposure to different concentrations of sulphide is shown in Fig. 1(a). The 96-h $LC_{50}$ calculated from probit transformation of the data was 700 ± 364 μM (95% confidence limits) total sulphide in oxygenated sea water at 14–18° C. In the short-term tolerance experiments, no killifish died in the controls and treatments up to 2 mM [Fig. 1(b)]. However, 50% of killifish exposed to 5 mM sulphide died in 3 h in one experiment, and in 6–8 h in the other. Half of the fish exposed to 8 mM sulphide died in 2–4 h. In the course of acute sulphide exposure, the fish at first huddled together with increased opercular and pectoral fin

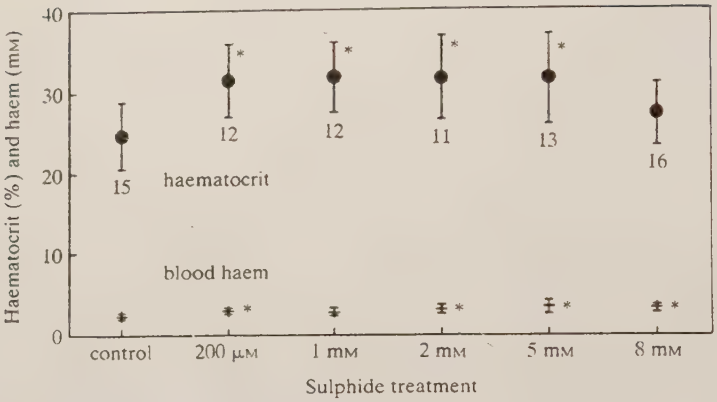

FIG. 2. Haematocrit and haem concentration (mean ± S.D.; sample sizes indicated on the haematocrit curve: same sample sizes for the haem curve) in fish from different sulphide treatments. Asterisks indicate significant differences from control values (ANOVA and two-tailed Dunnett's test. *q* values of $P<0.05$).

movement. This was followed by laboured ventilation, swimming to the surface and gulping air, and by frenzied attempts to leave the water. Poisoned fish lost equilibrium, swam awkwardly, ventilated long and deep, and finally turned over on their backs. Fish turned a darker colour during sulphide exposure.

Survival of killifish in 5 mM sulphide was improved by prior acclimation to 200 μM sulphide for 7 days. Newly-caught killifish suffered 75 ± 27% mortality (mean ± S.D., $n=3$ replicate aquaria, with a total of 64 fish); de-acclimated fish, 86 ± 5% ($n=3$, total 63 fish); and acclimated fish, only 23 ± 4% ($n=2$, total 40 fish). Mortality in the acclimated group was significantly different from the de-acclimated group, but neither was significantly different from the newly-caught group (one-way ANOVA and Tukey's test, *q* values of $P<0.05$).

## HAEMATOCRIT AND BLOOD HAEM CONCENTRATIONS

The haematocrit was 24·7 ± 4·1% and whole blood haem concentration was 2·4 ± 0·4 mM (mean ± S.D., $n=15$) in control killifish not exposed to sulphide. Significant increases in these parameters were observed in sulphide-exposed fish (Fig. 2). These increases occurred within the initial 2 h of sulphide exposure, and did not significantly change thereafter. Killifish dying in 8 mM sulphide did not show the haematocrit response.

## SHb OR $Hb^+$ FORMATION

Only two of 60 killifish (including 20 dead ones) examined after exposure to 200 μM to 8 mM sulphide showed some sulphhaemoglobin (SHb) in the bloodstream ($A_{618}/A_{576}$ ratio = 0·142–0·172). None of the fish examined showed any ferric haemoglobin ($Hb^+$) nor ferric haemoglobin sulphide ($Hb^+S$). Thus, death of killifish within 2–8 h in 5 mM and 8 mM sulphide was not due to significant SHb formation or impairment of oxygen transport.

Earlier experiments *in vitro* showed that killifish haemoglobin converted to SHb within minutes in 5 mM sulphide and within hours in 1 mM sulphide (Bagarinao &

Vetter, 1992). Thus, 1–5 mM sulphide is possibly the threshold concentration for impairment of oxygen transport in the killifish.

## SULPHIDE AND THIOSULPHATE IN TISSUES

In terms of the diffusible form of sulphide in sea water of pH 8·3, the concentrations used in the short-term tolerance experiments (200 μM to 8 mM) were equivalent to about 12–480 μM $H_2S$. If the blood equilibrated with the ambient sulphide and no oxidation occurred, it would have contained about this much sulphide. Figure 3 shows the sulphide and thiosulphate concentrations in the blood (a), spleen/heart (b) and liver (c) of fish from different sulphide treatments. Since the blood was used for other determinations (above), HPLC analysis of blood was done only for control fish, fish 6–8 h in the lethal 5 mM sulphide, and fish 11 days in non-lethal 200 μM sulphide from another experiment. Some sulphide (3 ± 1 μM, mean ± S.D., $n = 8$) was detected in blood from control fish, and this increased only two- to three-fold in fish from both the short-term 5 mM and the long-term 200 μM sulphide treatments. In contrast to the low sulphide concentrations, thiosulphate measured 71 ± 23 μM in controls, 303 ± 230 μM in the 200 μM treatment, and significantly higher at 853 ± 539 μM in the 5 mM treatment.

The heart/spleen and liver were analysed for more of the high-sulphide treatments [Fig. 3 (b, c)]. In these tissues, as in the blood, sulphide remained relatively low while thiosulphate increased much more with sulphide exposure. Fish in the lethal 5 mM and 8 mM sulphide treatments had, respectively, 30 ± 21 μM and 46 ± 24 μM sulphide in the heart/spleen, and 6 ± 9 μM and 35 ± 39 μM sulphide in the liver. Maximum thiosulphate concentrations noted were 956 μM in the heart/spleen and 680 μM in the liver in the 8 mM sulphide treatment.

Sulphide and thiosulphate concentrations in the blood and other tissues of fish from the ‘ nature/acclimation ’ experiment are shown in Table I. The brain had the highest sulphide concentration among the tissues examined. Such high sulphide level in the brain probably contributed to death of the fish. Blood sulphide concentrations were low and not significantly different among the three groups exposed to 5 mM sulphide nor between these and the controls. Thiosulphate concentrations were high and not significantly different among the three groups exposed to 5 mM sulphide; those from the newly-caught and acclimated groups were significantly elevated relative to the controls (one-way ANOVA and Tukey's test, $q$ values of $P < 0{\cdot}01$). Other tissues had lower thiosulphate levels than the blood. Statistical tests were not made for other tissues because of small sample sizes.

## INHIBITION OF CYTOCHROME *C* OXIDASE BY SULPHIDE

Figure 4(a) shows *in vitro* inhibition of cytochrome *c* oxidase of the killifish, as assayed in tissue homogenates. Inhibition of the enzyme was concentration-dependent over a range up to 5 μM sulphide. The $IC_{50}$ estimates ranged from 426–464 nM in the heart and brain, to 750 nM in muscle [Fig. 4(b)]. These inhibitory concentrations were very low, and showed that even a sulphide-tolerant fish had a sulphide-sensitive enzyme.

*In vivo* inhibition of cytochrome *c* oxidase was also observed during the experiment to determine shift to anaerobic metabolism. There was no mortality among the killifish during the 6-day 200 μM sulphide treatment, but 50% mortality during the 3-day 700 μM treatment. Cytochrome *c* oxidase was inhibited 50–90%

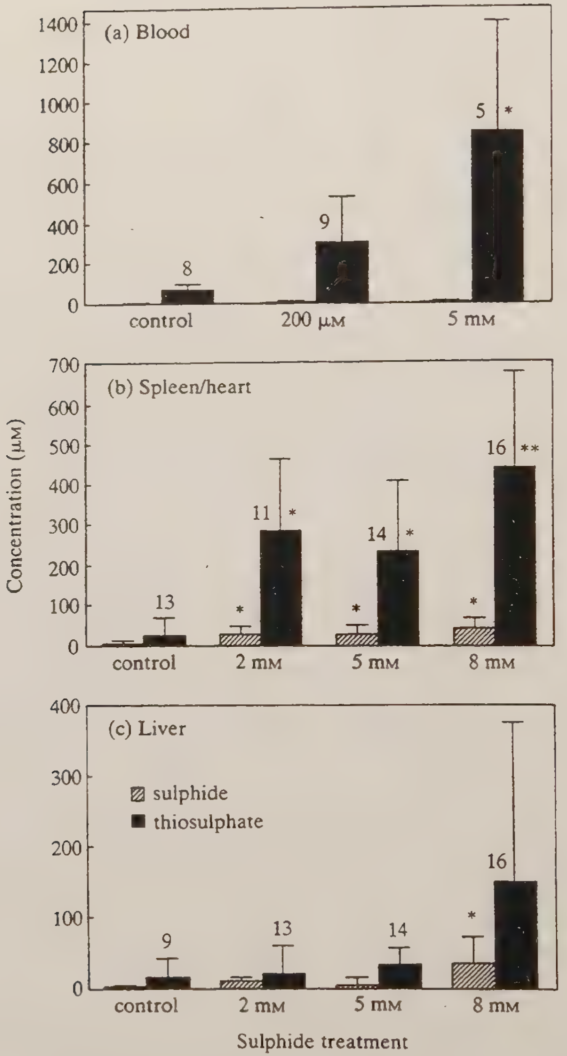

FIG. 3. Sulphide and thiosulphate concentrations in tissues of California killifish from the sulphide treatments (mean ± S.D.; sample sizes indicated on the bars). (a) Blood. Sulphide concentrations very low and not different between control and sulphide-exposed fish. Thiosulphate concentrations significantly elevated in fish from the 5 mM sulphide treatment. (b) Spleen/heart. Sulphide and thiosulphate concentrations significantly higher in fish from all treatments than in controls. (c) Liver. Sulphide concentration in fish from the 8 mM treatment significantly higher than in controls and the other sulphide treatments. No significant differences in thiosulphate concentration. Based on ANOVA and Tukey's test, *q* values of $P < 0.05$ (*) and $P < 0.01$ (**).

in the gill, 10–50% in the brain, and 0–50% in muscle (Table II). In fish that died in 700 μM sulphide, only the gill showed nearly complete inhibition (by 90%) to account for death. Liver activity did not seem inhibited and was even 50% stimulated in low sulphide. It must be noted that at least some reactivation of the inhibited enzyme may have taken place during preparation of homogenates and the 2–6 h between sampling and assay.

TABLE I. Sulphide and thiosulphate concentrations (mean ± S.D., $n$ = number of fish) in tissues of three groups of California killifish exposed to 5 mM sulphide for 6–8 h: newly-caught from the salt marsh, de-acclimated 1·5 months, and acclimated in 200 μM sulphide for 7 days. Some tissue samples were pooled (e.g. 5 in 1)

| Group | Tissue | *n* | Sulphide (μM) | Thiosulphate (μM) |
|---|---|---|---|---|
| Newly-caught, then 5 mM sulphide | | | | |
| | gill | 2 | 19 ± 1 | 61 ± 23 |
| | blood | 5 | 8 ± 7 | 853 ± 539 |
| | heart | 5 in 1 | 19 | 175 |
| | spleen | 5 in 1 | 10 | 427 |
| | brain | 3 | 85 ± 58 | 157 ± 104 |
| | intestine | 2 | 33 ± 4 | 75 ± 63 |
| | liver | 3 | 21 ± 12 | 32 ± 11 |
| | kidney | 5 in 2 | 9 ± 6 | 140 ± 4 |
| De-acclimated, then 5 mM sulphide | | | | |
| | gill | 3 | 40 ± 20 | 18 ± 13 |
| | blood | 5 | 8 ± 5 | 395 ± 389 |
| | heart | 5 in 1 | 8 | 77 |
| | spleen | 5 in 1 | 9 | 219 |
| | intestine | 1 | 13 | 10 |
| | liver | 1 | 6 | 17 |
| | kidney | 2 | 6 ± 1 | 75 ± 37 |
| Acclimated, then 5 mM sulphide | | | | |
| | gill | 3 | 18 ± 8 | 190 ± 107 |
| | blood | 5 | 10 ± 6 | 958 ± 516 |
| | heart | 5 in 1 | 30 | 329 |
| | spleen | 5 in 1 | 17 | 886 |
| | brain | 2 in 1 | 42 | 191 |
| | intestine | 1 | 16 | 111 |
| | liver | 3 | 24 ± 10 | 94 ± 54 |
| | kidney | 5 in 1 | 12 | 79 |
| Controls, newly-caught and no sulphide | | | | |
| | blood | 8 | 3 ± 1 | 71 ± 23 |
| | spleen | 2 | 3 ± 1 | 107 ± 22 |
| | kidney | 3 | 1 ± 1 | 21 ± 2 |

## ANAEROBIC GLYCOLYSIS DURING SULPHIDE EXPOSURE

Control unexposed killifish had 3·6 ± 1·4 mM lactate (mean ± S.D., $n = 30$) in the blood. When killifish were exposed to 200 μM sulphide for 6 days, anaerobic glycolysis came into play and blood lactate increased three-fold to a maximum of 10·8 ± 6·5 mM ($n = 3$) (Fig. 5). When killifish were exposed to 700 μM sulphide for 3 days, blood lactate increased 10-fold to 37·3 ± 4·2 mM ($n = 3$) at 72, but the fish died. Metabolic acidosis probably compounded the inhibition of cytochrome oxidase and caused the death of killifish in the 700 μM treatment. The lower lactate levels at 144 h in 200 μM sulphide were measured 8 h after the sulphide supply ran out (Fig. 5), and showed that fish stopped producing lactate.

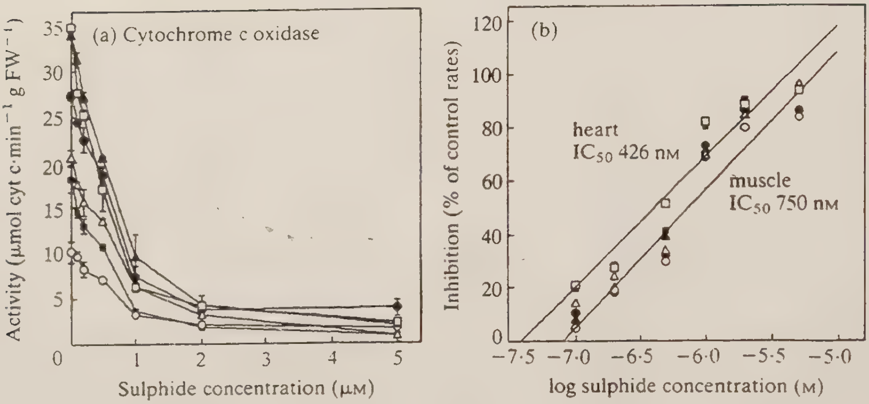

FIG. 4. Inhibition of cytochrome *c* oxidase in tissue homogenates of California killifish. (a) Enzyme activity against sulphide concentration [S], mean ± S.D. of three assays at each sulphide concentration using pooled homogenates from three fish. (b) Same data transformed as % inhibition against log [S] for estimation of the $IC_{50}$, the 50% inhibitory sulphide concentration. Only the two most extreme curves for the heart and the muscle are drawn. —●—, Gill; —■—, brain; —▲—, liver; —○—, muscle; —△—, kidney; —□—, heart.

Lactate dehydrogenase activity in killifish tissues assayed *in vitro* showed no significant change during sulphide exposure (Table II), and could not explain the increased lactate concentration in the blood. White muscle LDH had by far the highest activity, consistent with its primarily anaerobic function. In the sulphide exposure experiment, LDH activity was measured 5–8 h after removal of tissues from the fish (because cytochrome *c* oxidase was assayed first) and the delay probably affected the rates. When measured more promptly, killifish LDH activities were higher (muscle, 698 ± 149; liver, 170 ± 37; gill, 88 ± 20; brain, 141 ± 12; heart, 252 ± 13; blood, 13 ± 4 μmol pyruvate $min^{-1}$ g fresh $weight^{-1}$, $n = 4–5$).

### MITOCHONDRIAL OXIDATION OF SULPHIDE

Mitochondrial respiration was stimulated by 10–20 μM sulphide, with maximal rates around 15 nmol sulphide $min^{-1}$ mg $protein^{-1}$, and by 50 μM sulphide at half-maximal rates (Fig. 6), similar to earlier results (Bagarinao & Vetter, 1990). The toxic level for killifish mitochondria is therefore 50 μM sulphide. Mitochondrial sulphide oxidation capacity was significantly higher in fish acclimated in 500 μM sulphide for 10–12 days, compared with those acclimated in 200 μM, newly-caught, or de-acclimated for 1–2 months (Fig. 6). Killifish de-acclimated for 1–2 months showed rates the same as for newly-caught fish.

## IV. DISCUSSION

### MODEL OF SULPHIDE TOLERANCE

Consider the schematic in Fig. 7. Cytochrome *c* oxidase is located in the inner membrane of the mitochondria, within the cell, bathed by the blood, in the fish. Sulphide in the water has to diffuse across several barriers to reach the enzyme. Toxicity depends on the balance between the rate at which sulphide diffuses

TABLE II. Cytochrome *c* oxidase activity and lactate dehydrogenase activity in tissues of the California killifish during sulphide exposure. Values are mean ± S.D. ($n = 3$ fish, except control group $n = 6$). All fish were alive at sampling, except those in 700 μM sulphide at 72 h. Assays for cytochrome *c* oxidase were done 2–6 h after, and for LDH 5–8 h after removal of fish from aquaria

| Sample | Cytochrome *c* oxidase activity (μmol cyt *c* min$^{-1}$ g fresh weight$^{-1}$) | | | | LDH activity (μmol pyruvate min$^{-1}$ g fresh weight$^{-1}$) | | | |
|---|---|---|---|---|---|---|---|---|
| | Brain | Gill | Liver | Muscle | Brain | Gill | Liver | Muscle |
| Control fish | 12·5 ± 1·3 | 20·3 ± 3·6 | 11·5 ± 2·3 | 7·2 ± 0·9 | 89·8 ± 23·1 | 64·5 ± 9·9 | 114·7 ± 4·9 | 348·2 ± 95·6 |
| Fish in 200 μM sulphide | | | | | | | | |
| 2 h | 6·4 ± 2·0 | 7·4 ± 2·2 | 17·1 ± 1·4 | 3·4 ± 1·3 | 85·1 ± 2·0 | 96·2 ± 43·5 | 112·6 ± 22·9 | 440·6 ± 66·3 |
| 24 h | 6·4 ± 1·5 | 6·1 ± 1·8 | 17·2 ± 3·6 | 5·6 ± 2·1 | 102·4 ± 18·0 | 63·0 ± 8·6 | 128·8 ± 22·2 | 413·2 ± 129·5 |
| *Recovery | 11·8 ± 0·7 | 18·7 ± 1·8 | 11·1 ± 1·0 | 7·7 ± 2·2 | | | | |
| Fish in 700 μM sulphide | | | | | | | | |
| 2 h | 11·3 ± 1·7 | 11·3 ± 1·0 | 12·1 ± 2·6 | 6·2 ± 2·0 | 87·8 ± 3·5 | 49·3 ± 7·5 | 119·0 ± 27·2 | 368·4 ± 53·6 |
| 24 h | 11·7 ± 1·1 | 7·3 ± 0·4 | 11·1 ± 2·4 | 7·5 ± 1·9 | 72·6 ± 4·6 | 53·8 ± 6·4 | 107·2 ± 16·7 | 320·6 ± 50·7 |
| 72 h | 11·0 ± 1·7 | 2·4 ± 0·6 | 11·0 ± 1·0 | 5·3 ± 0·8 | 70·0 ± 5·1 | 38·3 ± 10·6 | 87·1 ± 18·9 | 407·9 ± 52·7 |

*Recovery 8 h after a 136-h sulphide exposure.

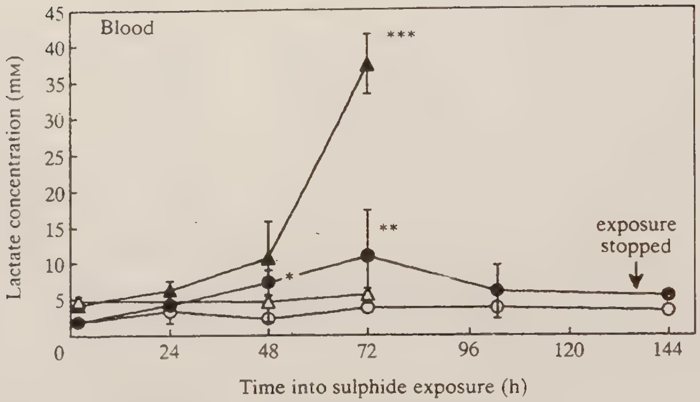

FIG. 5. Blood lactate concentrations in California killifish exposed to 200 and 700 μM sulphide. Control (unexposed) fish sampled at the same time and in the same manner as exposed fish to control for lactate production due to handling. Arrow indicates when the sulphide input stopped. Data for 144 h represent return to near-normal level. Asterisks indicate significant differences from respective controls and other time points, based on two-way ANOVA and Tukey's test, $q$ values of $P<0.05$ (*), $P<0.01$ (**), and $P<0.001$ (***). —▲—, 700 μM; —△—, control; —●—, 200 μM; —○—, control.

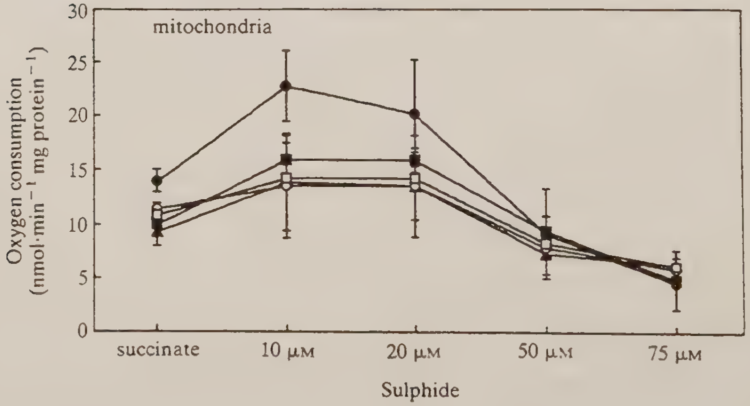

FIG. 6. Mitochondrial sulphide oxidation monitored as oxygen consumption rates (mean ± S.D., $n=3$ mitochondrial preparations, each from 7–10 fish) as a function of de-acclimation and acclimation. Mitochondria were removed from five groups of fish: (i) acclimated in 500 μM sulphide for 10–12 days; (ii) acclimated in 200 μM sulphide for 10–12 days; (iii) newly-caught from salt marsh; (iv) de-acclimated for 1 month; and (v) de-acclimated for 2 months. Mitochondrial sulphide respiration was significantly higher in the group acclimated in 500 μM sulphide for 10–12 days than in the other four groups (two-way ANOVA and Tukey's test, $q$ value of $P<0.05$). —●—, acclimated 500 μM; —■—, acclimated 200 μM; —▲—, newly-caught; —○—, de-acclimated 1 mo; —□—, de-acclimated 2 mo.

towards the enzyme (which depends on external sulphide concentration and pH) and the rate at which sulphide is detoxified by agents external to the enzyme. Any physiologically important sulphide detoxication system must be able to oxidize sulphide at a rate equal to the flux rate and must have sufficiently high affinity to

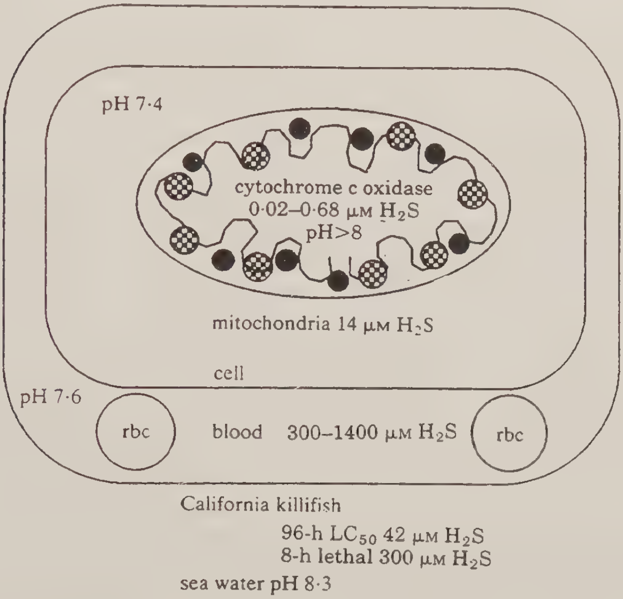

FIG. 7. Model of sulphide tolerance in the California killifish. Cytochrome *c* oxidase (larger circles) is located in the inner membrane of mitochondria. Cytochrome *c* (smaller circles) is located in the intermembrane space. The mitochondria are in cells, the cells are bathed by the blood, and the whole fish is exposed to sulphide in sea water. Sulphide has to diffuse across several barriers to reach the enzyme. Toxicity depends on the balance between the diffusion rate of sulphide towards the enzyme and the rate at which sulphide is detoxified by agents and mechanisms external to the enzyme. Drawn in the model are $H_2S$ concentrations recalculated from the total sulphide concentrations experimentally derived for the killifish in this and other papers (Bagarinao & Vetter, 1989, 1990, 1992).

rapidly reduce sulphide concentration to below that inhibitory to cytochrome *c* oxidase.

The cytochrome *c* oxidase of the killifish is inhibited by nanomolar sulphide. If assayed in homogenates, i.e. with the enzyme in a relatively ‘intact’ cellular environment, the 50% inhibitory concentration is 426–750 nM sulphide (Fig. 4). If assayed in tissue supernatants, i.e. with the enzyme detached from membranes and other cell components, the 50% inhibitory concentration is 24–184 nM sulphide (Bagarinao & Vetter, 1989). Isolated killifish mitochondria are 50% inhibited by 50 μM sulphide (Fig. 6; also Bagarinao & Vetter, 1990). Killifish blood is damaged (converted to SHb) at 1–5 mM sulphide *in vitro* (Bagarinao & Vetter, 1992). At the whole-animal level, 50% of the killifish tolerate 700 μM sulphide for 96 h, and 5 mM sulphide for 8 h (Fig. 1).

Toxic sulphide concentrations are better expressed as $H_2S$ since the latter is the diffusible form. $H_2S$ constituted 6% of total sulphide in sea water, pH 8·3, at which the whole-animal experiments were conducted, 28% at pH 7·4 at which mitochondria and haemoglobin were assayed, and 90% at pH 6·0 at which cytochrome *c* oxidase was assayed. Therefore, the whole-animal 96-h $LC_{50}$ for the California killifish is 42 μM $H_2S$ and the 8-h lethal concentration is 300 μM $H_2S$. The 50% inhibitory concentration for isolated mitochondria is 14 μM $H_2S$. The

50% inhibitory concentration for cytochrome *c* oxidase is 0·022–0·166 μM $H_2S$ in tissue supernatants and 0·383–0·684 μM $H_2S$ in tissue homogenates. The threshold concentrations for damage to haemoglobin is 280 μM $H_2S$ (over hours) or 1400 μM $H_2S$ (immediately). These values are plotted in the model in Fig. 7.

Two main conclusions may be derived from Fig. 7. First is that the mitochondria allow the killifish to withstand $H_2S$ concentrations two orders of magnitude greater than those that inhibit cytochrome *c* oxidase extracted from tissues. The sulphide concentration that inhibits mitochondria almost matches that which kills the fish. Thus, it appears that oxidative detoxication of sulphide by mitochondria is the chief mechanism behind the high sulphide tolerance of the killifish. If sulphide concentrations remain at relatively low concentrations in the water column, and they probably typically do in salt marshes, killifish mitochondria would be able to oxidize most of the sulphide before it reaches concentrations inhibitory to cytochrome *c* oxidase. Killifish mitochondria are capable of continuous detoxication of sulphide over several days (10–12 days in the 'nature-acclimation' experiment), and still do so upon subsequent isolation. Sulphide oxidation by killifish mitochondria is constitutive, and improved by acclimation (Fig. 6).

The sulphide-oxidizing mechanism in mitochondria probably consists of cytochrome *c* taking electrons from sulphide and passing them on to oxygen through cytochrome *c* oxidase. Based on the work of Moriarty & Nicholas (1969) and Nicholls & Kim (1981, 1982), we suggest that cytochrome *c* and cytochrome *c* oxidase are probably the 'sulphide oxidase', or components of the 'sulphide oxidase system' that some investigators have postulated (Powell & Somero, 1986; O'Brien & Vetter, 1990). The location of cytochrome *c* oxidase in the mitochondrial inner membrane, bathed in matrix fluid of $pH > 8$ fortuitously allows the enzyme to oxidize low concentrations of sulphide before being poisoned. The 0·02–0·68 μM $H_2S$ that is inhibitory to the enzyme is reached only when the matrix contains 0·33–11·33 μM total sulphide at pH 8·3. These high sulphide concentrations in the matrix in turn can only be reached when the concentrations outside the mitochondria are higher still.

Second is that killifish haemoglobin (blood) is relatively insensitive to sulphide and 'protects' cytochrome *c* oxidase by allowing the continued delivery of oxygen to mitochondria. The high threshold concentrations (280–1400 μM $H_2S$) required for SHb formation may explain why very few killifish exposed to high sulphide concentrations show any SHb in the blood. In killifish exposed to 5 mM sulphide in sea water pH 8·3, 300 μM $H_2S$ may be expected to occur in the blood by diffusion in the absence of sulphide uptake or detoxication. This concentration barely reaches the threshold for slow SHb formation and already equals the acute lethal concentration. Thus, the killifish die of sulphide poisoning not due to SHb formation.

Earlier studies have shown that killifish oxyhaemoglobin does not significantly oxidize sulphide, and that ferric haemoglobin, which does, occurs in negligible amounts (Bagarinao & Vetter, 1992). Other cellular factors may also be involved in the removal of free sulphide from solution, e.g. ferritin, disulphide-containing proteins, and S-methyltransferase (Baxter & van Reen, 1958; Cavallini *et al.*, 1970; Weisiger *et al.*, 1980). Their contribution is probably small because the reactions are non-specific. Although the killifish can shift to anaerobic metabolism during sulphide exposure (Fig. 5), glycolysis is of limited utility and eventually contributes to death.

## BIOCHEMICAL CHANGES DURING SULPHIDE EXPOSURE

Increases in the haematocrit and blood haem concentration in the killifish appear to be non-specific responses to stress induced by sulphide. Various studies suggest that haematological parameters may be useful indices of physiological response to environmental stress (Blaxhall, 1972). For example, teleosts respond to lowered dissolved oxygen or exercise by increasing the haem concentration (Cameron, 1970; Scott & Rogers, 1981). Such increases have been attributed to either water shifts from blood to tissue, or to compensatory haemoglobin production. Similarly, inhalation exposure of cats to 900 mg $l^{-1}$ $H_2S$ (=39 μM dissolved $H_2S$) for 5 min, and protracted exposure of rats to daily baths in 130–190 μM $H_2S$ for 20–30 min elevated the red blood cell counts and haemoglobin levels (in Beauchamp *et al.*, 1984). The significance of such haematological changes is not known. However, an increased blood haem concentration would enhance oxygen delivery to, and facilitate sulphide oxidation by mitochondria.

Occurrence of low sulphide and high thiosulphate concentrations in the tissues of fish exposed to 5 mM and 8 mM sulphide indicates that detoxication systems continue to work at these high concentrations, although for a limited time and at rates presumably lower than the sulphide influx rates. The highest thiosulphate concentrations are found in the blood, secondarily in blood-rich tissues such as the heart and spleen, and relatively low in the liver. Without evidence to the contrary, the blood may be assumed to oxidize sulphide. However, under nearly physiological conditions, the blood does not oxidize sulphide to thiosulphate at any appreciable rate, whereas liver mitochondria do so avidly (Bagarinao & Vetter, 1990, 1992). These results together with Fig. 3 and Table II suggest that thiosulphate produced in the liver (and probably other tissues) is readily transported into the blood. Accumulation of thiosulphate to high levels in the blood indicates that excretory mechanisms at best are slower than *in vivo* sulphide oxidation rates.

## ANAEROBIC METABOLISM

When California killifish are exposed to 200 μM sulphide (12 μM $H_2S$) for 6 days or to 700 μM sulphide (42 μM $H_2S$) for 3 days, cytochrome *c* oxidase is partially inhibited, anaerobic glycolysis comes into play, and blood lactate concentrations increase. The highest blood lactate concentrations (mean 37 mM) are observed in fish that had died in sulphide. These results are consistent with the high sulphide tolerance of the killifish, but also suggest that the upper limits of sulphide tolerance may be set by factors secondary to inhibition of cytochrome *c* oxidase, e.g. acidosis. When the channel catfish *Ictalurus punctatus* Rafinesque are exposed to 3 μM $H_2S$ for 30 min, cytochrome *c* oxidase in the brain and gills is inhibited 60–75%, and lactate concentrations in the blood increase more than three-fold (Torans & Clemens, 1982).

There is no evidence that the killifish has extraordinary anaerobic capacity. LDH activity per wet weight tissue does not increase during 3–6 days of sulphide exposure. The increase in blood lactate concentration during sulphide exposure is possibly due to a greater proportion of tissue mass shifting to anaerobic glycolysis with longer exposure. LDH activities in the killifish are not much different from those of other coastal fishes, after allowing for assay temperature, use of homogenates versus supernatants, intraspecific scaling with size, and differences in swimming and feeding habits (Sullivan & Somero, 1980; Castellini & Somero, 1981). In the congener *Fundulus heteroclitus* L., serum lactate concentration is 3·5 mM, and LDH activities are 227 units g wet weight$^{-1}$ in liver and 300 units g wet weight$^{-1}$ in skeletal muscle supernatants assayed at 25° C (Greaney *et al.*, 1980).

Lactate accumulation during anaerobic glycolysis leads to tissue acidosis (Pörtner *et al.*, 1984; Fievet *et al.*, 1987), a problem particularly for white muscle, which generates most of the lactate and has generally poor capillary circulation. Thus, there is need for adequate buffering capacity in muscle. Indeed, Castellini & Somero (1981) found similarly high buffering capacities in skeletal muscles of 11 species of actively foraging pelagic fishes and 10 species of diving mammals. The killifish probably has comparable muscle buffering capacity with these animals, and is able to continue anaerobic glycolysis for a period of days.

Shift to anaerobic metabolism during sulphide exposure may be a more important physiological strategy for sulphide tolerance among benthic invertebrates, which employ a greater variety of adaptive strategies and metabolic pathways (Shumway *et al.*, 1983; Oeschger & Storey, 1990; Levitt & Arp, 1991).

## CONSTITUTIVE BASIS OF SULPHIDE TOLERANCE AND EFFECT OF ACCLIMATION

The 'nature/acclimation' experiments on the California killifish have shown that survival in 5 mM sulphide, *in vivo* detoxication of sulphide to thiosulphate, and mitochondrial respiration on sulphide, are not different between newly-caught and de-acclimated fish, but are significantly improved by prior acclimation in 200 or 500 μM sulphide. In fact, killifish held in sulphide-free water for 6 months tolerate subsequent exposure to 700 μM sulphide for 3 days, and 200 μM sulphide for at least a week (in the separate experiment on anaerobic metabolism).

That de-acclimation or holding of killifish for months in the laboratory in sulphide-free water does not eliminate the ability of both whole fish and isolated mitochondria to oxidize sulphide is possibly because the sulphide-oxidizing enzyme system (cytochrome *c* and cytochrome *c* oxidase) is constitutive. The ability of mitochondria to oxidize sulphide has now been documented across four phyla (Bartholomew *et al.*, 1980; Lloyd *et al.*, 1981; Powell & Somero, 1986; Bagarinao & Vetter, 1990), likewise indicating a constitutive basis.

That acclimation improves fish survival in an otherwise lethal sulphide concentration, and enhances mitochondrial sulphide oxidation rates, is probably due to adjustments in the amounts or catalytic rates of cytochrome *c* and cytochrome *c* oxidase, or to a host of other factors that still have to be investigated. Acclimation is thus one more modifier of sulphide tolerance, which has been shown previously to vary with species, habitat, life stage or size, temperature, dissolved oxygen levels and pH (Theede *et al.*, 1969; Adelman & Smith, 1972; Smith & Oseid, 1974; Broderius *et al.*, 1977; Shumway *et al.*, 1983; Vetter *et al.*, 1987; Bagarinao & Vetter, 1989; Vismann, 1990; Levitt & Arp, 1991). Extensive research on other environmental factors (such as temperature, hypoxia and heavy metals) have shown that tolerance of animals to high levels is improved by prior exposure to lower levels. Cellular and molecular adjustments are made by the animal during the acclimation period (Shaklee *et al.*, 1977; Greaney *et al.*, 1980; Hobson & Birge, 1989), usually months, such that it can survive subsequently an otherwise lethal exposure. The longest sulphide acclimation period in this study was 12 days because it was a difficult experiment to do in the long term (large amounts of sulphide are needed in the flow-through exposure system and sulphide solutions have to be made up fresh every day).

In conclusion, the remarkably high tolerance of California killifish to sulphide can be explained chiefly by mitochondrial sulphide oxidation. Killifish exposed to sulphide shift to anaerobic metabolism, but fish with the most lactate die. Killifish blood does not catalyse sulphide oxidation significantly, or binds sulphide at environmental (low) sulphide concentrations. Sulphide tolerance and mitochondrial sulphide oxidation in the killifish have a constitutive basis and are improved by prior acclimation.

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# Predation on walleye pollock (*Theragra chalcogramma*) eggs and yolk-sac larvae by pelagic crustacean invertebrates in the western Gulf of Alaska

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## ABSTRACT

Immunological detection of yolk protein was used to assess predation by pelagic amphipods (gammarid and hyperiid), mysids, and euphausiids on eggs and yolk-sac larvae of walleye pollock *Theragra chalcogramma* during 1988 and 1989. Consumption estimates were made on the basis of frequency of positive immunoassays, assay detection times (gut clearance time), predator abundance, and spatial overlap of predators and prey. From our results gammarid amphipods and euphausiids were important predators on eggs and yolk-sac larvae, respectively. Gammarid amphipods alone consumed about 14% of the standing stock of pollock eggs in 1989. These results were compared with those from clearance rate experiments of predators feeding on pollock eggs in 300-l bags. In general, clearance rate estimates of egg consumption were lower than those determined from gut contents.

**Key words:** walleye pollock, *Theragra chalcogramma*, predation, fish eggs, immunoassay

## INTRODUCTION

Predation is believed to be one of the major sources of mortality for marine fish eggs and larvae (Hunter, 1984; Bailey and Houde, 1989, and references therein). However, predation in the field, including identification of the major predators and how many prey they are eating, is poorly understood owing to difficulties of assessment.

Several methods are used to study invertebrate predation upon early stages of marine fishes, each with advantages and drawbacks. Laboratory-derived clearance rates of predators feeding on fish eggs and larvae have been applied to field estimates of predator abundances (Bailey and Yen, 1983; Monteleone and Duguay, 1988). This method has numerous problems; for instance, small-scale spatial overlap of prey and predators is not easily replicated in the laboratory, and it is difficult to extrapolate results under laboratory conditions to those in the sea. Predation also can be estimated from the difference between total and nutrition-related mortality (Hewitt et al., 1985; Leak and Houde, 1987); drawbacks to this method are that predators remain unidentified and both empirical estimates may be relatively imprecise, resulting in a low degree of confidence in predation estimates.

Gut contents of potential predators can be examined either visually or serologically. Difficulties with these methods include variable digestion rates, gut voiding, and feeding during net capture. Visual examination of guts has been particularly useful for studying fish predation on eggs (Hunter and Kimbrell, 1980; Brodeur et al., 1991), but larvae are believed to be digested very rapidly. This method has also been useful for estimating predation of gelatinous zooplankton on eggs and larvae (Moller, 1984; Purcell, 1989; Purcell and Grover, 1990). Serological techniques are most useful for marine crustacean predators that macerate their prey, which renders direct visual identification impossible (Feller et al., 1979). Theilacker et al. (1986) and Theilacker (1988) have used serological methods to study predation by euphausiids on northern anchovy *Engraulis mordax* eggs and yolk-sac larvae.

We studied invertebrate predation on walleye pollock (*Theragra chalcogramma*) eggs and yolk-sac larvae from Shelikof Strait, the major spawing area in the western Gulf of Alaska (Kendall and Picquelle, 1990). Peak spawning occurs during a two-week period in early April. Eggs are located near the bottom (150–250 m) in a concentrated patch (Kendall and Kim,

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1989) and hatch after about 14 days at a water temperature of 5–6°C. Yolk-sac larvae (3–4 mm) move toward the surface and are generally distributed in the upper 150 m; they are still quite concentrated and located downstream from the eggs (Incze et al., 1989).

Mortality of walleye pollock eggs and early-stage larvae is high and variable. Daily egg mortality has been estimated at 10–30% (Kim and Gunderson, 1989). Estimates of daily larval mortality range from 6% to 15% (Incze et al., 1989; Yoklavich and Bailey, 1990). It has been proposed, although the evidence is scarce, that predation is the major source of walleye pollock egg (Kim and Gunderson, 1989) and larval mortality (Walline, 1983).

The objectives of the present study were (1) to identify invertebrate predators of walleye pollock eggs and yolk-sac larvae using serological techniques, (2) to estimate predation rates in the field, and (3) to compare predation rates in the field to those determined from clearance rates in 300-l bags.

## MATERIALS AND METHODS

### *Field methods*

The area of the main walleye pollock spawning aggregation in Shelikof Strait was initially sampled in a 18.5 × 18.5 km grid to define the distribution of pollock eggs and larvae during ichthyoplankton surveys in 1988 and 1989. Following these initial presurveys, plankton collections were made in areas of high egg and yolk-sac larval densities. Cruises were conducted aboard the NOAA ship *Miller Freeman*. Cruises from April 1 to 13, 1988 and from April 5 to 16, 1989, were termed "egg cruises," since eggs were predominant in catches. A cruise from 16 April to 2 May 1988 was termed the "yolk-sac cruise" even though eggs were also present, since hatching was occurring and sampling was directed to capture predators feeding on yolked larvae.

A 1-$m^2$ mechanically operated Tucker trawl with 505-$\mu$m mesh nets was deployed to sample predators at specific depth strata where the highest concentrations of eggs and yolk-sac larvae were expected to occur (Kendall and Kim, 1989; A. Kendall, NMFS, Seattle, personal communication). For egg predators the net was towed obliquely from 250 to 150 m. For yolk-sac larvae the net was towed obliquely from 150 m to the surface. Depth of sampling was monitored with an electronic bathykymograph. Volume of water sampled was estimated with a flowmeter in each net. To examine diel differences in predation, we tried to distribute the sampling effort equally between day and night.

Larger predators also were sampled during the yolk-sac cruise in 1988 using a 5-$m^2$ Methot frame trawl (Methot, 1986) equipped with a 2 × 3 mm oval mesh net. Oblique tows were made from 150 m to the surface.

Feeding on eggs and larvae in the codend of the nets (Hirota, 1984; Nicol, 1984) is a potential problem in sampling. A 1.5-mm mesh codend was used on all nets to allow pollock eggs and larvae to pass through the codend while predators were retained.

The contents of the codend were emptied into a sorting tray containing a slurry of iced seawater, and most of the large crustacean predators were removed quickly (<10 minutes), placed in microcentrifuge tubes, and stored at −80°C. The remaining sample was preserved in 5% buffered formalin in seawater. All specimens ≥5 mm (maximum dimension) in the crustacean groups Euphausiacea, Mysidacea, and Amphipoda (Hyperiidea and Gammaridea) were later identified to species and enumerated. Abundance was standardized to number per 10 $m^2$.

Because many predators make extensive vertical migrations extending outside the depth of our sampling, we adjusted predator abundance on the basis of the percentage of the total predator abundance that overlapped with egg or larval vertical distributions during the diel period. We approximated the vertical distribution of the dominant species in the four invertebrate groups and walleye pollock eggs and 3–4 mm larvae, presumed to be yolk-sac stage, using abundance data from four (two day and two night) MOCNESS tows (Wiebe et al., 1976), which were collected over eight depth strata from the surface to 250 m on April 21 and 24, 1988. Mesh size was 153 $\mu$m.

### *Laboratory methods*

For immunoassays, individual frozen specimens were placed on a microscope slide and allowed to thaw briefly. Digestive tracts were dissected from each specimen and placed into Protein Extraction Buffer (PEB; 10 mM Tris-HCl, 1 mM EDTA, pH 7.4). Gut fullness was visually estimated and recorded. Guts were transferred into 20 $\mu$l of chilled PEB and homogenized with a Duall disposable tissue grinder (1.5-ml volume; Kontes of California, Hayward, CA). Ten microliters of homogenate were spotted onto 0.45-$\mu$m nitrocellulose paper in a microfiltration apparatus and allowed to drain. The blots were kept at 4°C until the membrane appeared to be dry, usually 12–18 hours.

The nitrocellulose membrane was removed from the filtration apparatus and blocked in Blotto-wash (5% nonfat dried milk, 0.05% Tween-20, 0.01% antifoam A, phosphate buffered saline, pH 7.4; modifed from

Theilacker et al., 1986) for up to 24 hours. The remaining protocol for washes and rinses is described by Theilacker et al. (1986) with the following modifications. Ten percent normal goat serum was used in both the conjugate antibody preblock and the conjugate antibody incubation. Because nonspecific binding of euphausiid gut contents appeared to occur with the secondary antibody, two blots were run simultaneously; one was incubated with both the primary and the secondary antibody, and the second was incubated with the secondary antibody only. The primary antibody was a polyclonal rabbit-anti-pollock egg-yolk protein IGG fraction produced in New Zealand rabbits (Merati et al., unpublished manuscript). The primary antibody used in the immunoblots was diluted 1 : 5000 in Blottowash. The secondary antibody was a 1 : 3000 dilution of goat-anti-rabbit alkaline phosphatase (Biorad Laboratories, Richmond, CA). Invertebrate specimens whose guts were allowed to clear for 24 hours and walleye pollock eggs and yolk-sac larvae were used as negative and positive controls, respectively. The reaction was visualized by color development with NBT (*p*-nitro-blue tetrazolium chloride) and BCIP (5-bromo-4-chloro-3 indyl phosphate *p*-toluidine salt).

### *Consumption estimates*

The number of walleye pollock eggs or yolk-sac larvae consumed per 10 m$^2$ per day (C) by each predator species ($j$) was calculated by

$$C_j = \frac{A_j \cdot P_j \cdot N_j \cdot V_j}{D_j},$$

where

$A$ = predator abundance per 10 m$^2$,

$P$ = proportion of invertebrate guts testing positive for antigen,

$N$ = number of eggs or yolk-sac larvae per gut (assumed = 1),

$V$ = correction factor for incomplete vertical overlap (as described above),

$D$ = detection time of yolk protein in guts (d).

Detection time ($D$) of yolk protein was estimated by observing predators placed in jars with walleye pollock yolk-sac larvae. Predators that fed successfully were placed in jars containing either filtered seawater or algae at 6°C (average water temperature in the field) and were sacrificed at hourly intervals. These predators were frozen in liquid nitrogen and assayed for egg proteins.

The vertical overlap correction factor ($V$) was estimated from the percentage of predators found at each depth stratum ($i$) during the day ($P_{di}$) and night ($P_{ni}$), adjusted to the same depth stratum ($A_i$) where eggs and larvae are found by the following formula:

$$V = \frac{H_d \sum_{i=1}^{8} \min(P_{di}, A_i) + H_n \sum_{i=1}^{8} \min(P_{ni}, A_i)}{24},$$

where $H_d$ and $H_n$ are the hours of daylight and darkness during the sampling period.

Total consumption ($C_t$) for each life history stage of walleye pollock was estimated by summing over the four predator groups ($j$):

$$C_t = \sum_{j=1}^{4} C_j \cdot S,$$

where $S$ is stage duration (assumed to be 14 days for eggs and 7 days for yolk-sac larvae; Bailey and Stehr, 1986). The proportion of the total egg population consumed was estimated by dividing the number of eggs consumed by the number estimated to be available in the plankton at the nearest stations from the grid survey. This was not possible for yolk-sac larvae because of potentially high rates of extrusion through the 505-$\mu$m mesh nets (Lo, 1983).

### *Mesocosm study*

Clearance rate experiments of predators feeding on walleye pollock eggs were conducted at sea during the 1988 and 1989 egg cruises. Polyethylene bags (300 l) were filled with filtered seawater, immersed in a large water bath at ambient temperature (3–4°C), and covered with a black tarp to simulate light at depth. Most (36) experiments were conducted in daytime for 9–12 hours, although a few (4) experiments were conducted for 20–24 hours. Four predator types (gammarids, hyperiids, euphausiids, and mysids) were removed live from Tucker trawls and held in seawater at 4–6°C. Eggs were extruded from trawl-caught adults, fertilized, and reared at 4–6°C. Eggs were counted into each bag, and 5–6 predators of one type were added. Initial egg densities were 0.01, 0.1, and 1 l$^{-1}$ (low, medium, and high densities). Maximum egg densities estimated from oblique bongo tows in the Shelikof spawning area are from 0.2 to 0.6 l$^{-1}$, and actual densities over a narrower depth range would be considerably higher. From two to five replicate experiments were conducted for each density and predator type. Additional bags (one at low, two at medium, and three at high egg densities) without predators were used as controls for counting errors. Eggs were essentially neutrally buoyant. After each experiment, water from each bag was siphoned through a 333-$\mu$m mesh filter, the empty bag was rinsed three times, and the rinse water was likewise filtered. Clearance rates ($l \cdot \text{predator}^{-1} \cdot \text{day}^{-1}$) were calculated as

$$C = \{(\ln(n_i) - \ln(n_f)) \cdot V\} \cdot (NT)^{-1},$$

where $n_i$ is the initial egg density (number $\cdot$ $l^{-1}$), $n_f$ is the final egg density (number $\cdot$ $l^{-1}$), $V$ is the volume, $N$ is the predator number, and $T$ is the duration of the experiment in days (from Marin et al., 1986).

## RESULTS

Seventeen likely zooplankton predator species were caught in Tucker trawls; mean densities ranged from 0.15 to 864.18 $m^2$ (Table 1). Except for euphausiids, the major categories were dominated by one species. Specimens frozen for gut analyses were not identified by species prior to immunoassays in 1988. However, on the basis of the sorted portion of catches, we assume that almost all gammarids were *Cyphocaris challengeri*; most hyperiids were *Themisto pacifica*; most mysids were *Meterythrops robusta*; and all euphausiids were *Euphausia pacifica, Thysanoessa spinifera*, and *T. inermis* in 1988.

Because there was little difference in vertical distribution among predator species within each major grouping, we have combined these distributions (Fig. 1). Walleye pollock eggs mainly (>80%) were distributed below 150 m. Most (>75%) small, presumably yolk-sac, pollock larvae (3–4 mm S.L.) were located above 150 m. There were marked diel changes in vertical distributions of all predators except mysids, which were caught near-bottom in both night and day tows. Gammarids were mostly near-bottom in daytime and more evenly distributed in midwater at night. Most euphausiids were caught above 150 m in day and night tows, with a shift toward the surface at night. Hyperiids were distributed nearly uniformly through the water column, especially at night.

From the egg cruises of both 1988 and 1989, 11–16% of gammarid and hyperiid amphipods tested positive for walleye pollock egg yolk proteins (Tables 2 and 3). Mysids in 1988 and 1989 and euphausiids in 1988

**Table 1.** Frequency of occurrence (F.O.) and mean ($\bar{x}$) and standard deviation (S.D.) of abundance by cruise per 10 $m^2$. Abundances include only individuals >5 mm in maximum dimension. ($n$ = number of collections by cruise)

| | Egg cruise, 1988 | | | Yolk-sac cruise, 1988 | | | Egg cruise, 1989 | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | F.O. ($n$ = 21) | ($\bar{x}$) | S.D. | F.O. ($n$ = 18) | ($\bar{x}$) | S.D. | F.O. ($n$ = 6) | ($\bar{x}$) | S.D. |
| Gammaridea | | | | | | | | | |
| *Cyphocaris challengeri* | 85.71 | 86.19 | 75.83 | 77.78 | 67.01 | 107.30 | 100.00 | 864.18 | 537.24 |
| *Atylus tridens* | — | — | — | — | — | — | 16.67 | 4.40 | — |
| Hyperiidea | | | | | | | | | |
| *Themisto pacifica* | 90.48 | 69.52 | 43.98 | 83.33 | 21.92 | 22.11 | 83.33 | 45.74 | 47.35 |
| *Themisto libella* | 4.76 | 0.15 | — | — | — | — | — | — | — |
| *Hyperia medusarum* | 4.76 | 1.01 | — | — | — | — | — | — | — |
| *Primno macropa* | 61.90 | 8.11 | 10.33 | 5.56 | 3.52 | 10.33 | 83.33 | 25.48 | 24.60 |
| Mysidacea | | | | | | | | | |
| *Meterythrops robusta* | 76.19 | 66.53 | 75.10 | 61.11 | 274.56 | 345.98 | 100.00 | 365.87 | 258.72 |
| *Holmesiella anomala* | 9.52 | 1.21 | 4.47 | — | — | — | — | — | — |
| *Archeomysis grebnitzkii* | — | — | — | 5.56 | 0.27 | — | — | — | — |
| *Xenocanthomysis* spp. | — | — | — | 5.56 | 22.19 | — | — | — | — |
| Euphausiacea | | | | | | | | | |
| *Euphausia pacifica* | 71.42 | 34.17 | 98.35 | 77.78 | 35.53 | 27.11 | 50.00 | 9.63 | 10.67 |
| *Thysanoessa spinifera* | 9.52 | 20.65 | 77.39 | 72.22 | 95.98 | 116.52 | 33.33 | 4.99 | 8.53 |
| *Thysanoessa inermis* | 23.81 | 20.85 | 59.02 | 72.22 | 113.89 | 139.88 | 66.67 | 121.10 | 241.23 |
| *Thysanoessa raschii* | 4.76 | 0.70 | — | 27.77 | 4.05 | 12.76 | — | — | — |
| *Thysanoessa inspinata* | 4.76 | 0.66 | — | 38.89 | 13.05 | 24.80 | — | — | — |
| *Thysanoessa longipes* | 28.57 | 6.30 | 11.73 | 22.22 | 3.72 | 9.80 | 33.33 | 16.03 | 11.41 |
| *Tessarabrachion oculatum* | 4.76 | 0.61 | — | — | — | — | — | — | — |

**Figure 1.** Vertical distribution of walleye pollock *Theragra chalcogramma* eggs and yolk-sac larvae and predator taxa from four MOCNESS tows (two day and two night) in the western Gulf of Alaska, April 21 and 24, 1988.

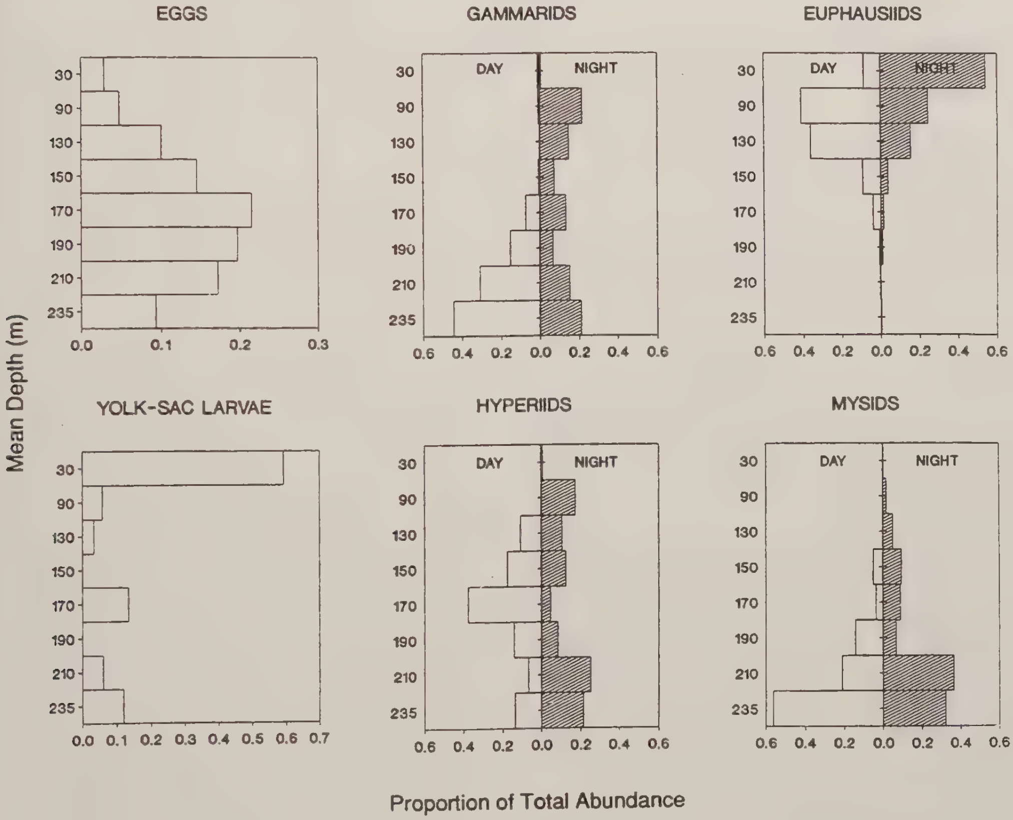


**Table 2.** Estimates of total number of eggs consumed by zooplankton predators during 1988 in relation to the number available per 10 m² of sea surface area.

| Taxa | Mean abundance | Number analyzed | Positive reaction | Vertical overlap | Number consumed | Percent consumed |
|---|---|---|---|---|---|---|
| Gammaridea | 86.19 | 103 | 0.144 | 0.577 | 602.5 | 5.39 |
| Hyperiidea | 69.52 | 114 | 0.113 | 0.708 | 467.3 | 4.18 |
| Mysidacea | 66.53 | 80 | 0.038 | 0.528 | 110.7 | 0.99 |
| Euphausiacea | 83.95 | 140 | 0.028 | 0.287 | 57.0 | 0.51 |
| Total | | | | | 1237.5 | 11.06 |

Table 3. Estimates of total number of eggs consumed by zooplankton predators during 1989 in relation to the number available per 10 m$^2$ of sea surface area.

| Taxa | Mean abundance | Number analyzed | Positive reaction | Vertical overlap | Number consumed | Percent consumed |
|---|---|---|---|---|---|---|
| Gammaridea | 867.14 | 55 | 0.164 | 0.577 | 6877.4 | 14.30 |
| Hyperiidea | 71.23 | 20 | 0.150 | 0.708 | 635.4 | 1.32 |
| Mysidacea | 365.87 | 93 | 0.054 | 0.528 | 872.4 | 1.81 |
| Euphausiacea | 141.15 | 2 | 0.028[1] | 0.287 | 95.3 | 0.20 |
| Total | | | | | 8385.2 | 17.44 |

[1] Insufficient number analyzed for 1989, taken from 1988 analysis.

tested 3–5% positive. From the yolk-sac cruise in 1988, 15.5% of euphausiids tested positive for yolk proteins, and only 1.7% of gammarids had positive reactions (Table 4). We found no evidence of day/night differences in the incidence of pollock egg yolk proteins in guts of any of the four predator groups (chi-square test: all $P > 0.05$).

Detection time of yolk protein in euphausiid guts varied between 1 and 4 hours, and all detection of antigen ceased after 3–4 hours for hyperiid and gammarid amphipods. There was no discernable difference in digestion time between predators placed in filtered seawater and predators placed in seawater with algae. We have therefore made the simplifying, and conservative, assumption that detection time was equal to 4 hours for all predators (including mysids, which were not available to be tested).

In 1988, gammarid and hyperiid amphipods were the most significant consumers of pollock eggs (5.39 and 4.18%, respectively). In 1989, all predators except hyperiids were much more abundant, and these higher abundances, along with higher incidences of predation, resulted in an increase in the number of eggs consumed by all predator groups from 11.06% (0.8% day$^{-1}$) in 1988 to 17.44% (1.2% day$^{-1}$) in 1989 (Tables 2 and 3). Gammarid amphipods were again the most important consumers of eggs.

From the yolk-sac cruise in 1988, euphausiids were the most important consumers of yolk-sac larvae (Table 4), contrasting with the findings of the major predators on eggs in 1988 (Table 2).

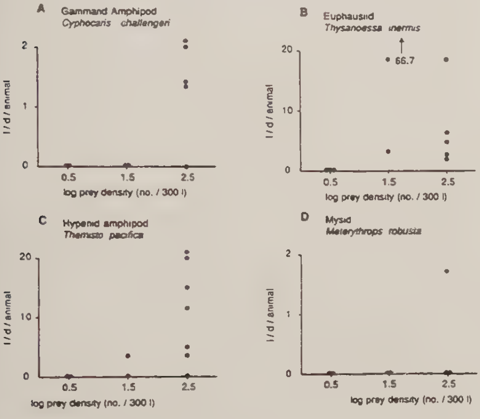
From bag experiments, clearance rates of the four predator types tested were greater at highest egg densities (i.e., at the three densities tested, the rates were not constant as expected) (Fig. 2). We suggest that this may have been because of the very low probability of a successful encounter at the lowest egg densities over the duration of the experiment. For example, at the highest egg densities the mean euphausiid clearance rate was only 0.3 l$^{-1}$ hour$^{-1}$ individual$^{-1}$; therefore during a 12-hour experiment the probability of five euphausiids capturing an egg at the low density of 0.01 eggs l$^{-1}$ is only about 16.6% (18 l cleared out of 300 l, with a probability of 0.01 that any one liter contains an egg: $1 - (99/100)^{18} = .1655$).

The number of eggs consumed in the sea, deter-

Table 4. Estimates of total number of yolk-sac larvae consumed by zooplankton predators during 1988 per 10 m$^2$ of sea surface area.

| Taxa | Mean abundance | Number analyzed | Positive reaction | Vertical overlap | Number consumed |
|---|---|---|---|---|---|
| Gammaridea | 67.01 | 59 | 0.017 | 0.322 | 15.1 |
| Hyperiidea | 25.47 | 51 | 0.078 | 0.331 | 27.8 |
| Mysidacea | 296.96 | 22 | 0.048 | 0.255 | 151.4 |
| Euphausiacea | 266.22 | 250 | 0.155 | 0.383 | 665.1 |
| Total | | | | | 859.4 |

**Figure 2.** Clearance rates of crustacean predators feeding on walleye pollock *Theragra chalcogramma* eggs in 300-l bags. The duration of experiments was 9–24 hours.



mined from mean and maximum clearance rates and observed densities of eggs and predators for 1988 and 1989, was compared with those from gut assays (Table 5). The number of eggs consumed from clearance rate experiments is 3–10 times lower than estimates derived from gut assays, except for euphausiids, which tend to have higher estimates based on clearance rates.

Immunoassays were conducted on guts of predators from the bag experiments. From 12 experiments in which no eggs were missing from the bags, 72 animals that presumably had eaten no eggs tested negative in immunoassays. From seven experiments in which eggs were consumed from the bags, four animals out of 42 tested positive.

## DISCUSSION

Invertebrate predators are an important source of mortality for fish eggs and larvae (Hunter, 1981; Bailey and Houde, 1989), but estimates of their impact have been made only recently (Theilacker et al., 1986; Theilacker, 1988; Purcell, 1985, 1989; Purcell and Grover, 1990). In this study, we surveyed a range of abundant crustacean predators using an immunological assay and made initial estimates of predation potential in order to focus future efforts. Our results indicate that gammarid and hyperiid amphipods are important predators on walleye pollock eggs and that euphausiids are significant predators on yolk-sac larvae of this species.

Biological and physical factors can influence predation rates (Purcell, 1985; Bailey and Houde, 1989); among these factors is the spatial and temporal overlap in distribution of predators and prey (e.g., Frank and Leggett, 1982). We found that the vertical overlap of walleye pollock eggs and larvae with crustacean invertebrate predators had a major effect on estimates of predatory impact. Euphausiids, which occur mostly in the upper 150 m, overlapped minimally with eggs but overlapped substantially with yolk-sac larvae; euphausiids were the major predator group on yolk-sac larvae but ate relatively few eggs. Gammarid and hyperid amphipods, on the other hand, are most concentrated at middle or lower depths, overlap to a greater extent with the developing eggs, and apparently consume them at relatively high rates.

There are many factors that can influence estimates of predation from both laboratory experiments and field assay of gut contents. Predation rates from analysis of predator gut contents were generally much higher than estimates from laboratory-derived clearance rates.

**Table 5.** Comparison of total egg consumption estimated from clearance rate experiments and gut content immunoassays in 1988 and 1989 per 10 m$^2$ over the 14-day egg residence time. Range of egg consumption estimates are based on mean and maximum clearance rates for each predator taxon. Mean egg abundance used to calculate consumption from clearance rates was 11,000 per 10 m$^2$ in 1988 and 48,000 per 10 m$^2$ in 1989. Predator abundances and corrections for vertical overlap are the same as in Tables 2 and 3.

| | | | 1988 | | 1989 | |
|---|---|---|---|---|---|---|
| Taxa | Mean clearance rate (l/day) | Maximum clearance rate (l/day) | Estimated no. eaten | Estimated from guts | Estimated no. eaten | Estimated from guts |
| Gammaridea | 0.8 | 2.0 | 6–15 | 602 | 282–675 | 6877 |
| Hyperiidea | 7.1 | 15.1 | 53–114 | 467 | 240–512 | 635 |
| Mysidacea | 0.6 | 1.8 | 3–10 | 110 | 78–233 | 872 |
| Euphausiacea | 7.1 | 18.9 | 26–70 | 57 | 192–515 | 95 |

There are several plausible reasons. First, capturing animals at depth with nets and bringing them to the surface could influence their physical condition and behavior, thus limiting their capabilities. Second, both *Cyphocaris* and *Themisto* tend to get trapped at the water–air interface in laboratory containers, effectively halting their feeding activity on suspended eggs. We did not notice this for individuals in the bags, but it remains a possible factor. Third, although the eggs appeared to be neutrally buoyant and well distributed in rearing jars, they may have been segregated from the predators in the bags, with predators accumulated at the sides, bottom, or top of the bags. This was probably a significant problem with mysids, which tend to remain near or on the bottom. From previous experiments conducted in 1-l jars, these same predators either did not eat fish eggs or ate them at low rates (Theilacker and Lasker, 1974; Bailey and Yen, 1983; Bailey and Stehr, 1986); however, they readily ate yolk-sac fish larvae. Confinement in small jars may also affect predator behavior, decreasing their ability to detect or handle fish eggs. De Lafontaine and Leggett (1987) found that for gelatinous predators, decreasing container size increased predation rates. Experiments by Monteleone and Duguay (1988) had different results; they found that clearance rates of the ctenophore *Mnemiopsis leiydi* decreased with decreasing container size. Predator species have different mechanisms for detecting and capturing prey; therefore their responses to container sizes are expected to vary.

Conversely, the immunoassays could have overestimated predation rates if there was codend feeding, if there were false positives, or if digestion rate estimates were too high. We used a codend with a mesh size that is considerably larger than the diameter of walleye pollock eggs, which should have minimized the capture of eggs and any codend feeding. Crustaceans used in bag experiments that did not consume eggs did not have any false positive reactions in the immunoassays. In addition, based upon animals that did consume eggs in bag experiments, the assays appeared to be relatively conservative. Our antibody-antigen reactions of predator gut contents was considerably weaker and more difficult to interpret than results of dilute yolk protein–antibody reactions. Antigenicity of the yolk protein was probably diminished during the digestion process. We suggest that in future studies, developing antibodies against partly digested (with trypsin or other enzyme) antigen be compared with antibodies against whole antigen. In addition, the reaction of predator guts with goat-anti-rabbit secondary antibody was a problem that we attempted to control by checking this reaction alone for each gut assayed. In retrospect, a nonreacting secondary antibody should be sought for future studies.

It was interesting that clearance rates estimated at low egg densities, similar to *in situ* values (0.01–0.1 eggs $l^{-1}$), were not constant, but rather increased with prey density. This observation could result from predators with low feeding rates combined with the short (10–24 hour) duration of experiments because the probability of ingesting prey is low. Experiments done with gelatinous zooplankton predators that feed upon fish eggs and larvae at higher rates and in which duration of experiments was longer (24–48 hours) have demonstrated constant clearance rates (Monteleone and Duguay, 1988; De Lafontaine and Leggett, 1987; Fancett and Jenkins, 1988); on the other hand, these are predators with linear or Type-I (Holling, 1959) functional responses. Animals that have a sigmoidal functional response, such as predators whose feeding activity decreases at low prey density, would be expected to have low clearance rates at low prey density.

Gut detection times of egg proteins were variable and not obviously influenced by alternative prey or continuous feeding. Immunoassay detection is based on the presence of antibody binding sites on the egg proteins. Digestion may influence the nature of these binding sites, and thus antigen digestion rates could be fast in relation to an assay based on total protein content. Thus our estimates of 4 hours for gut residence times is likely to be conservative. However, even halving detection times, thus doubling predation mortality, would not substantially alter our conclusions. Our antibody does not cross-react with algae or invertebrate eggs but does cross-react with yolk proteins from other fish species; in our field studies, cross-reactions with other fish eggs is an insignificant problem, since walleye pollock eggs comprised over 99% of all eggs caught in April cruises of 1988 and 1989 (Alaska Fisheries Science Center ichthyoplankton files, unpublished data).

Gut content assays may be conservative for several other reasons. First, predators may be defecating during the capture process. However, because the assay can detect nanogram amounts of egg protein, even a trace presence of yolk in the gut would be detected. Paradoxically, few predators from net catches were observed to have melanin in their guts compared with animals feeding in the laboratory. Although eggs have little melanin content until the eyes develop just before hatching, the absence of melanin may indicate that defecation occurred during the capture process. Second, animals testing positive in the assays were assumed to have eaten only one prey during the digestion interval; this provides the most conservative estimate and is supported by the low rate of feeding in the bag experiments. Finally, it is difficult to estimate the abundance of evasive predators such as euphausiids; problems with abundance estimates would apply equally to estimates of egg consumption from gut content and clearance rate methods.

Our estimates of daily egg mortality due to predation by pelagic crustaceans (0.8–1.2% $day^{-1}$) are low in relation to estimates of total egg mortality for walleye pollock (10–30% $day^{-1}$ from Kim and Gunderson, 1989). The immunoassay results, as discussed above, may be conservative, but other sources of mortality could also be significant. For example, pelagic fishes may consume large numbers of eggs, or nonpredatory mortality (e.g., developmental abnormalities) could be substantial. Predation rates from gut assays were still considerably higher than those estimated from bag experiments, indicating that bag studies may underestimate the impact of predators. Because both the bag and immunoassay results depend on good estimates of predator abundance, we recommend improvements in this area. Our results also demonstrated the importance of vertical overlap of predators and prey, and this should be included as a component of future predation studies.

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# APPENDIX A
# ANNOTATED LIST OF SHARK ATTACKS IN THE HAWAIIAN ISLANDS, 1779-1993, BY GEORGE H. BALAZS

The following list provides a case-by-case factual synopsis of the 104 known shark attacks in the Hawaiian Islands, from the earliest recorded event in 1779 to the most recent one in June 1993. Available information is also summarized here in separate tables covering the activity of the victim, the month of the attack and the species of shark involved.

Prior to the publication of my first assembled shark attack list in 1981 (co-authored with Alan K.H. Kam), no consolidated historical information of this nature was available for Hawaii. Old cases of shark attack were located through comprehensive searches of books, newspaper files and other sources. This is an ongoing process. I am grateful to Gail Bartholomew, Leighton Taylor, John Naughton and others for their continuing assistance in uncovering valid cases from Hawaii's past that warrant addition to the list.

Since 1981 nearly all new cases have been readily identified at the time of their occurrence when they appeared in Hawaii's newspapers and television reports. In many instances I have been able to personally interview the victim, or the last person to see the victim alive, in order to record first-hand accurate information to the extent that it is known. Autopsy and police reports have also been used to contribute meaningful data. A list of the literature and other sources used to document each case, too long to include here, has been deposited in the Pacific Collection of Hamilton Library, University of Hawaii at Manoa.

Forty-four (42.3 percent) of the 104 cases on the following list are tabulated as having involved a fatality. However, nine (20.5 percent) of these forty-four fatalities are considered to have been "likely" due to drowning or other causes, which was then followed by shark bite, dismemberment, and/or consumption. No cases have been included on this list in which a person was known with certainty to have been dead prior to being bitten by a shark. Cases involving fatality present special challenges to a compiler when there is no first-hand witness to the death, and medical evidence is inconclusive or nonexistent. In each such case I have used the best available information to render a professional judgment in assigning one of four footnoted categories to the fatality. It is recommended that the reader become familiar with these footnotes before studying the list. The inclusion on this list of cases where the cause of death is uncertain or unknown is both valid and consistent with the scientific protocol followed by several other registers of shark attacks compiled elsewhere worldwide, including Australia.

Sixty (57.7 percent) of the 104 cases involve persons who survived the shark attack. For cases occurring during recent years, these individuals have been available to describe the event in detail on a first-hand basis. The circumstances and documentation given by them provide valuable insight that can be used to surmise what may have transpired in fatal cases where no witness was present. For example, read and compare case number 75 with case number 95.

The criteria and style used to compile the list of shark attacks in Hawaii has been patterned after the International Shark Attack File (ISAF), which was first assembled in the late 1950s with funding from the Office of Naval Research. A tabular summary of the ISAF list was published in the 1963 classical reference book entitled *Sharks and Survival,* edited by Dr. Perry Gilbert. Later, in 1973, an analysis of data involving 1,165 cases in the ISAF was published by Dr. David Baldridge in his report "Shark Attack Against Man." The ISAF is currently maintained under the auspices of the American Elasmobranch Society at the Florida Museum of Natural History, with Dr. George H. Burgess as curator. Updated and revised versions of the shark attack list for Hawaii are regularly forwarded by the compiler for inclusion and use by the ISAF.

Cases of shark attack shown in the following list involve some manner of physical injury to the person that resulted from a shark. Cases in which "only" the person's equipment was attacked (bitten), or aggression was displayed without harmful contact to a person, are not included. In this respect, the list for Hawaii is more conservative and differs from certain other lists compiled elsewhere (including the ISAF). On those registers, attacks solely on boats, surfboards and other items are included even though no injury to a human took place. Significant cases of this nature have indeed occurred in Hawaii. At a later date they will be catalogued into a separate list. An example of one such cases is as follows. In October 1990 Greg Filtzer was lying on his nine-foot-long surfboard in Hanalei Bay on Kauai when a twelve-foot tiger shark bit the board and violently pulled it and Greg backwards underwater. In the process the shark ripped off a fourteen-inch-wide piece of the surfboard. Without so much as a scratch, Greg miraculously paddled to shore after the shark released the board. The entire event was witnessed by a companion on a surfboard next to him.

In Dr. Gilbert's book, *Sharks and Survival,* the following notable comment appears on page 466: "Although it is probable that most people would regard a statement of the rarity of attacks in the statistical sense as correct and reasonable, it appears that people in general are less willing to accept a risk involving sharks than greater risks of almost any other kind." This is not surprising, considering that the two words most commonly used in relation to shark attack are "fear" and "apprehension." Most people gain no comfort from being told they are at greater risk from bee stings and car accidents than from shark attack. Statistics alone have a way of reducing people to simple numbers devoid of the personal tragedies and, in some cases, incredible courage associated with shark attack in Hawaii. The following list speaks for itself in that each case presented is an individual story, not simply a statistic.

In the state of Hawaii's 1972 report covering the last systematic shark control and research program conducted in Hawaiian waters, it is stated that "Sharks normally receive negligible fishing pressure and since they function as apex predators in the sea's food pyramid they can increase to maximum density. A dense shark population coupled with growing popularity of water sports activities increase the probability of shark encounters." Although shark attacks are statistically few in number, the validity of this statement now, twenty years later, appears to hold true. There is no question that sharks must be rationally conserved as a fishery resource and not "eradicated" as some have suggested. But at the same time the issue of public safety in Hawaiian waters, coupled with fear and apprehension among residents and tourists alike, must not be neglected.

George H. Balazs
June 1993

## SHARK ATTACK CASES IN THE HAWAIIAN ISLANDS BY ACTIVITY

| Activity | Fatal | Non-Fatal | Total |
|---|---|---|---|
| Swimming/snorkeling | 8 | 15 | 23 |
| Spearfishing while snorkeling | 1 | 5 | 6 |
| Scuba diving | 3 | 1 | 4 |
| Spearfishing while scuba diving | 2 | 0 | 2 |
| Hard hat diving | 0 | 1 | 1 |
| Surfboarding | 2 | 15 | 17 |
| Body (boogie) boarding | 2 | 3 | 5 |
| Sail boarding | 0 | 1 | 1 |
| Body surfing | 1 | 2 | 3 |
| Surfing on an air mattress | 1 | 0 | 1 |
| Floating on an inner tube (w/lobsters) | 0 | 1 | 1 |
| Wading | 0 | 1 | 1 |
| Fell into sea from shore or swept out to sea | 16 | 0 | 16 |
| Fell off boat or boat capsized | 3 | 1 | 4 |
| Net fishing | 0 | 4 | 4 |
| Crabbing | 1 | 2 | 3 |
| Removing shark from fishing line or gaff | 0 | 3 | 3 |
| Dynamite fishing | 1 | 0 | 1 |
| Fishing (type unknown) | 2 | 1 | 3 |
| Activity unknown | 1 | 4 | 5 |
| Total | 44 | 60 | 104 |

## SHARK ATTACK CASES IN THE HAWAIIAN ISLANDS BY SPECIES OF SHARK

| Shark species | No. fatal | No. non-fatal | Total No. cases |
|---|---|---|---|
| Tiger shark | 3 | 6 | 9 |
| Great white | 1 | 1 | 2 |
| Hammerhead | 0 | 2 | 2 |
| Cookie Cutter | 1 | 0 | 1 |
| Subtotal | 5 | 9 | 14 |
| Unknown species, large | 20 | 10 | 30 |
| Unknown species, small | 1 | 8 | 9 |
| Unknown species, unknown size | 18 | 33 | 51 |
| Subtotal | 39 | 51 | 90 |
| Total | 44 | 60 | 104 |

## SHARK ATTACK CASES IN THE HAWAIIAN ISLANDS BY MONTH FOR THE YEARS 1779-1993

| Month | Fatal | Non-Fatal | Total |
|---|---|---|---|
| January | 3 | 2 | 5 |
| February | 2 | 5 | 7 |
| March | 2 | 5 | 7 |
| April | 7 | 9 | 16 |
| May | 2 | 1 | 3 |
| June | 3 | 7 | 10 |
| July | 4 | 2 | 6 |
| August | 4 | 3 | 7 |
| September | 2 | 5 | 7 |
| October | 1 | 6 | 7 |
| November | 4 | 4 | 8 |
| December | 3 | 6 | 9 |

Note: For 92 cases in which the month of attack is known. Cases occurred during the month of April every year for the 6-year period, 1986-1991.

## GENERAL OUTCOME OF SHARK ATTACK CASES IN THE HAWAIIAN ISLANDS, 1779-1993

Compiled by George H. Balazs
(Following categories established by H. D. Baldridge, 1973 in "Shark Attack Against Man")

| | No. of cases | % |
|---|---|---|
| Non-fatal. | 60 | 57.7 |
| Fatal, body or parts thereof recovered, death considered direct result of shark-inflicted wounds. | 10 | 9.6 |
| Fatal, no details reported. | 2 | 1.9 |
| Assumed fatal, body not recovered, no personal gear recovered. | 3 | 3.0 |
| Fatal, body or parts thereof recovered, not known if death was direct result of shark-inflicted wounds. | 17 | 16.3 |
| Fatal, body or parts thereof recovered, death not considered direct result of shark-inflicted wounds. | 9 | 8.6 |
| Assumed fatal, body not recovered, personal gear was recovered. | 3 | 2.9 |
| Total | 104 | 100.0 |

# SHARK ATTACK CASES IN THE HAWAIIAN ISLANDS INVOLVING FATALITIES

| | | | | | Overall | | |
|---|---|---|---|---|---|---|---|
| Years | Direct fatality (a) | Likely direct fatality (b) | Other causes (c) | Cause of fatality Unknown (d) | No. fatal | No. non-fatal | Total no. cases |
| 1990-present | 2 | 3 | 2 | | 7 | 10 | 17 |
| 1980-89 | | 2 | 3 | 4 | 9 | 15 | 24 |
| 1970-79 | | | 1 | 2 | 4 | 8 | 12 |
| 1960-69 | | | 1 | 3 | 3 | 5 | 8 |
| 1950-59 | 3 | | 1 | 3 | 7 | 7 | 14 |
| 1940-49 | | | | 1 | 1 | 5 | 6 |
| 1930-39 | | | | 1 | 1 | 5 | 6 |
| 1920-29 | 1 | | | | 1 | 2 | 3 |
| 1910-19 | | 1 | | 1 | 2 | 1 | 3 |
| 1900-09 | 2 | | 1 | 3 | 6 | 2 | 8 |
| 1779-1899 | 2 | | | 1 | 3 | 0 | 3 |
| Total | 10 | 6 | 9 | 19 | 44 | 60 | 104 |
| | 22.7% | 13.6% | 20.5% | 43.2% | | | |

a = Death directly due to shark attack.
b = Death likely due to shark attack.
c = Death likely due to drowning or other trauma followed by shark attack.
d = Insufficient information upon which to base an opinion as to cause of death.

# ANNOTATED LIST OF SHARK ATTACK CASES IN THE HAWAIIAN ISLANDS 1779 - 1993

(* = FATALITY INVOLVED)

COMPILED BY GEORGE H. BALAZS

HONOLULU LABORATORY, SOUTHWEST FISHERIES SCIENCE CENTER

NATIONAL MARINE FISHERIES SERVICE, NOAA

| Case no. | Date | Location | Victim | Circumstances |
|---|---|---|---|---|
| 1*[a] | 1779 | Maliu, Hawaii | Nu'u-anu-pa'ahu | Young male gashed on one side of buttocks after being pursued while surf boarding. Subsequently suffered "great pain" and died at Pololu. |
| 2*[a] | 1828 | Lahaina, Maui | Male | "A man out riding surf at 'Uo was killed by a shark which bit off his limbs and left his body floating." Attack witnessed by a number of Hawaiian chiefs. |
| 3*[d] | 2 June 1886 | Hamakua, Hawaii | Two females | Washed into the sea while fishing from shore; one woman found bitten (fatal), the other woman disappeared. |

COMPILER'S OPINION AS TO CAUSE OF FATALITY

[a] Fatality *directly* attributed to shark attack.

[b] Fatality *likely* attributed to shark attack.

[c] Fatality *likely* attributed to another cause (drowning, etc.) besides shark attack which was followed by mutilation or dismemberment by shark or sharks.

[d] *Insufficient information upon which to base an opinion as to cause of death,* although mutilation and/or dismemberment by sharks had occurred. Fatality may have been directly attributed to shark attack, or may have resulted from another cause. This category also includes an absence of any witnesses or the absence of sufficient body remains to determine cause of death by medical autopsy.

| Case No. | Date | Location | Victim | Circumstances |
|---|---|---|---|---|
| 4[*c] | 14 July 1900 | Makapuu Point, Oahu | Emil Uhlbrecht and an unidentified person | Believed to have drowned when carried out to sea while hunting sea shells with companions. "A thorough search was made for the body for several days." Victim's foot with skin and flesh intact "in a fair state of preservation" was found in the stomach of an 11-ft 9-in shark hooked on the night of 8/17/00 off Kakaako, Honolulu, by John Kinipeki. Positive identification of victim made by Mrs. Uhlbrecht, based on an ingrown toe nail. Human pelvis and femur, blackened and totally denuded of flesh, were also recovered from the shark's stomach. These bones were thought to be from a different person, probably one of several Chinese fishermen lost over board in the harbor during past months. |
| 5 | Early 1900's | Inter-Island Dry Dock at Kakaako St. Honolulu | Emil A. Berndt | Young boy severely chafed when a large shark swam between his legs. |
| 6[*a] | 8 Aug. 1902 | Kalihi, Oahu | Young male | Pulled under while crabbing; both arms amputated. |
| 7[*d] | 1904 | Honolulu, Oahu | Male | Partial remains of swimmer who had disappeared two days earlier off Diamond Head found in the stomach of a "monstrous shark." Body was complete from the waist down with the exception of one leg. Shark also contained ducks, tin cans, and wood. |
| 8[*d] | 1907 | Pepeekeo, Honomu, Hawaii | Male | Bitten while fishing. |
| 9 | 8 Oct. 1907 | Kalepolepo, Kihei, Maui | Male | Arm amputated at the elbow while retrieving fish caught in net. |
| 10[*a] | 17 Jan. 1908 | Mana, Kauai | Male | Pulled under while gathering fish stunned by dynamite. |
| 11[*d] | 10 Apr. 1909 | Pauwela, Maui | Mrs. Ah Kim Chong | Nineteen-year old woman reported to have been swept away by waves while gathering opihi along the rocky shore line. Search party saw a large shark |

| Case no. | Date | Location | Victim | Circumstances |
|---|---|---|---|---|
| | | | | devour what appeared to be part of the missing woman's body. |
| 12 | Apr. 1910 | Pearl Harbor, Oahu | Martin Lund | Unprovoked attack on a hard hat diver. Authenticity questioned. |
| 13[*d] | 1910 | Hilo, Hawaii | Male | Bitten while fishing. |
| 14[*b] | 3 Mar. 1914 | Honomu, Hawaii | Okomoto | Washed into the sea while picking opihi and attacked by two large sharks. |
| 15 | 28 Sept. 1922 | Keawanui, Kamalo, Molokai | Male | Bitten while inspecting wharf. |
| 16 | 7 Apr. 1926 | Hilo Bay, Hawaii | Mrs. Leonard Carlsmith | Severely bitten while swimming 25 yards from shore near the Hilo Yacht Club at 5:30 p.m. "The shark with one bite terribly lacerated her right leg from the heel to the thigh. The calf of her leg was torn nearly to shreds, and the part of her limb above the knee was laid open to the bone." A long necktie was applied as a torniquet to her leg as soon as she was brought to shore. "Anesthetics" were required twice at the hospital in order to treat the wounds. According to the victim, the shark that bit her "had a mouth about three feet wide". |
| 17[*a] | 18 May 1926 | Haleiwa, Oahu | William J. Goins | Gave a sudden shriek then disappeared while swimming at Haleiwa; remains of body found in 12.5-ft great white shark caught off Kahuku. |
| 18 | 13 June 1931 | Pearl Harbor, Oahu | Lieutenant Williamson | End of one of the victim's fingers amputated while using a gaff to bring a 10-ft tiger shark aboard a boat after harpooning it. Shark also bit in half the 2-in oak pole of the gaff. The following items were found in the shark's stomach: hind leg of a mule, two bathing suits nearly digested, soldier's belt buckle, a pint of button's, two horse shoes, corner of a wooden soapbox, anchor chain, two small anchors, and assorted bolts, nails, and copper fittings. |

| Case no. | Date | Location | Victim | Circumstances |
|---|---|---|---|---|
| 19*d | 2 Sept. 1931 | Kahala, Oahu | George Gaspar | Swept out to sea by strong currents while fishing; remains of body found in 18-ft shark caught off Barbers Point. |
| 20 | 16 Feb. 1932 | Lahaina, Maui | Male | Sailor from U.S. Navy vessel *Saratoga* bitten while swimming about 1 mile off Mala Wharf. Two wounds each 6-inches long were inflicted. |
| 21 | 4(?) Sept. 1936 | Lahaina, Maui | young male | Leg "badly cut" requiring 19 stitches at the Lahaina Hospital. Swimming with several other children near the "old wharf" when a shark was sighted. Victim disappeared underwater for a few seconds then came to the surface and "made a frantic effort for land". "A large shark was seen again the following morning". |
| 22 | 30 Dec. 1936 | Honokohau, Maui | John Kekuhi | Bitten on the thigh while diving under water trying the retrieve the body of a drowning victim wedged between two rocks. Three deep gashes sustained which required hospitalization. Shark reported to be 20-ft. |
| 23 | 4 Oct. 1939 | Kaneohe Bay, Mokapu, Oahu | James Akina | Bitten on hand by 5-ft shark while spear fishing in shallow water. |
| 24 | 1 July 1941 | Nanakuli, Oahu | Hisao Shimoto | Bitten on arm while removing 100-lb shark from fishing line. |
| 25*d | 5 Apr. 1943 | McGregor Point, Maui | Leonard Gant | Disappeared while swimming with three companions after the small boat they were canoeing swamped in high seas. Swamping occurred three miles from shore. Victim vanished shortly before reaching land after he fell behind the other swimmers. On 4/29/43, the "decomposed remains" of the victim's "right forearm" and "brightly colored swimming trunks" were "found in the stomach of a 16-ft shark" caught in turtle nets set out at night "near the Koa house" by Kihei fisherman Alex Akina. Shark's stomach also contained a piece of newspaper dated 3/25/43. |

| Case no. | Date | Location | Victim | Circumstances |
|---|---|---|---|---|
| 26 | 1943 | Midway, Northwestern Hawaiian Islands | Male | Unprovoked attack, but unable to determine circumstances. |
| 27 | 1943 | Midway, Northwestern Hawaiian Islands | Male | Unprovoked attack, but unable to determine circumstances. |
| 28 | 27 June 1947 | Makaha, Oahu | Valentine Limatoc | Bitten while spearfishing with six other men. |
| 29 | 19 Sept. 1948 | Makapuu, Oahu | Noah Kalama | Bitten on leg while swimming. |
| 30*[c] | 16 Jan. 1950 | Kahakuloa, Maui | Gilbert S. Hotta | Swept into the sea with two companions by a large sudden wave while fishing at night from the rocky base of an over hanging cliff. Another companion (Wayman Fujimoto) managed to cling to the rocks when the wave hit. The partial remains of Gilbert Hotta were recovered from a "huge shark" caught on the morning of 1/19/50 by rescue workers searching the immediate area. The "badly battered remains" of one of the other missing fishermen (Harold Fujimoto) was also recovered floating nearby. The body of the third fisherman (Hideo Tamura) was never found. |
| 31*[d] | 25 June 1951 | Kapehu Beach, Laupahoehoe, Hawaii | Alejandro Nodura | Swept out to sea while fishing from shore. Victim seen in shark's mouth. |
| 32*[d] | 3 Aug. 1952 | Ala Moana, Oahu | Shigeichi Kawamura | Missing while swimming; shark bite found on right side of body. |
| 33*[a] | 3 Dec. 1952 | Maile, Oahu | Gerbacio Solano | Bitten on arm while swimming from fishing boat; shark reported to be in excess of 22 ft. |
| 34 | 18 Feb. 1953 | Barbers Point, Oahu | James S. Takeuchi | Bitten on hand while removing shark from net. |
| 35 | 4 July 1953 | Kaula Rock | David Crick | Fell off boat while fishing; bitten on leg. |
| 36*[a] | 26 July 1953 | Maile, Oahu | Harold Souza | Bitten on thigh while spearfishing close to shore; 10-ft shark observed. |

| Case no. | Date | Location | Victim | Circumstances |
|---|---|---|---|---|
| 37 | 2 Sept. 1953 | Waiau, Pearl Harbor, Oahu | Daniel Gonsalves | Bitten on leg and foot by 5-ft hammer head shark while crabbing. |
| 38[*d] | 8 Apr. 1954 | Wailupe, Oahu | Gordon S. Chun | Missing while fishing from shore; body recovered in mutilated condition. |
| 39 | 1954 | Molokai | Severino | Unprovoked attack, but unable to determine circumstances. |
| 40 | Apr. 1955 | Hilo, Hawaii | Kanematsu Oshiro | Bitten on hand while fishing from boat. |
| 41 | 20 Sept. 1955 | East Molokai | Phillip C. Diez | Bitten on arm while swimming. |
| 42[*a] | 13 Dec. 1958 | Lanikai, Oahu | William S. Weaver | Leg amputated while surfing on an air mattress near Twin Islands; 15- to 25-ft shark (believed to be tiger shark) observed near body when fire-rescue personnel recovered it 2 hours later. No additional bite marks present on the body. |
| 43 | 1950's | Waikiki, Oahu | David Lloyd | Provoked attack, but unable to determine circumstances. |
| 44 | 27 Feb. 1960 | Makena, Maui | John Benjamin | Severe lacerations obtained while spearfishing. |
| 45[*d] | 27 Dec. 1960 | Maile Point, Oahu | Harold Riley | Swept out to sea while net fishing; 20-ft shark observed attacking victim; body recovered off Nanakuli. |
| 46 | 2 Aug. 1961 | Pearl Harbor, Oahu | Kazuhiko Kato | Bitten on hand by 8-ft shark while net fishing. |
| 47[*d] | 8 Apr. 1963 | Hapuna Beach, Hawaii | Roy C. Kametani | Washed into the sea while picking opihi; parts of body recovered. |
| 48 | 12 Apr. 1963 | Awili, South Kona, Hawaii | Aiona Aka | Bitten on leg and foot while surfing; 12- to 15-ft shark observed. |
| 49[*d] | 20 Sept. 1967 | Kailua Bay, Oahu | Male | Victim lost at sea when boat capsized between Oahu and Molokai; remains of body found in 11-ft tiger shark. |
| 50 | 9 Mar. 1969 | Makaha, Oahu | Licius Lee | Bitten on leg while surfing; identified as great white shark based on teeth marks in surfboard; dead whale recently removed from the area. |

| Case no. | Date | Location | Victim | Circumstances |
|---|---|---|---|---|
| 51 | 11 Nov. 1969 | Barbers Point, Oahu | D. R. McGinnis | Bitten on tank while scuba diving for lobsters; abrasions on arms and legs and cut on ankle resulting from contact with shark. |
| 52[*c] | 31 Mar. 1970 | Waimea Bay, Oahu | Ernie Reathaford | Swept out to sea while body surfing; 15- to 18-ft shark observed. |
| 53 | 24 Oct 1970 | Brennecke Beach, Poipu, Kauai | James C. Mattan | Bitten on shoulder and arm while body surfing. |
| 54 | 16 Mar. 1972 | Waihee, Wailuku, Maui | Adam Gomes, Jr. | Bitten on leg while spearfishing. |
| 55 | 17 Aug. 1972 | Waimanu, Honokaa, Hawaii | Eric Fotherby | Bitten on arm by 8-ft shark while spearfishing. |
| 56 | 9 Jan. 1973 | Hookipa Beach, Paia, Maui | Robert Sterling | Bitten on leg while surfboarding close to shore; 4 to 6-ft shark observed in area: wound required 100 stitches. |
| 57 | 18 Dec. 1973 | Kalama Beach, Kihei, Maui | Gary W. Floyd | Bitten on leg while swimming close to shore. |
| 58 | 10 June 1976 | Kamaole Beach, Park No. 1, Kihei, Maui | Donald Gard | Bitten on foot and leg by 3- to 5-ft shark while swimming. |
| 59[*d] | 16 July 1976 | Mahaulepu, Koloa, Kauai | Stephen C. Powell | Missing while scuba diving; lower remains of body recovered. |
| 60[*c] | 1976 | Off Lahaina, Maui | Danson Nakaima | Apparently passed out while scuba diving for black coral at a depth of 180 ft. About 30 large sharks seen near partially devoured remains of the body. |
| 61 | 21 Apr. 1977 | Kaanapali, Maui | Ruskin Vest | Bitten on arm by 4-ft. shark while swimming close to shore. |
| 62 | 27 Nov. 1978 | Ewa, Oahu | Wendell Cabunoc | Severely bitten on arm while surfboarding; 8-ft shark observed. |
| 63[*d] | 1979(?) | South Kohala, Hawaii | Elderly male | Disappeared while fishing from shore. Fire Department divers only found a hand and a flashlight. Note: No known literature documentation. |

| Case no. | Date | Location | Victim | Circumstances |
|---|---|---|---|---|
| 64 | 4 Aug. 1980 | Puamana, Lahaina, Maui | Mark Skidgel | Bitten on left side of body while resting on a body board 40 ft from shore; identified as 14-ft tiger shark; wound required 52 stitches. |
| 65*[d] | 24 May 1981 | Haena Beach Park, Kauai | Roger B. Garletts | Missing while scuba diving at a depth of 60- to 80-ft; only diving equipment recovered, including shredded wet suit bearing numerous tooth marks. Victim reportedly spearfishing in murky, choppy water. |
| 66*[c] | 12 June 1981 | Honolii Pali, Hilo Bay, (Alae Point), Hawaii | Preston D. Soley | Retrieval of floating body hindered by 4-ft shark. Autopsy showed that death was probably from drowning. One-third of body missing due to bites by at least four sharks. |
| 67*[d] | 24 Aug. 1981 | Keaukaha, Hilo, Hawaii | Ernest Watson | Disappeared while fishing from shore. Leg found 7 days later wedged in rocks 150 yd offshore. |
| 68 | 9 Nov. 1981 | Laau Point, Molokai | Leo A. Ohai | Bitten on hand while untangling crab-trap line from propellor. Seven-foot shark had followed the boat for 3 days and reportedly was very unusual looking with a "flat head". |
| 69 | 13 Dec. 1981 | Nimitz Beach, Barbers Point, Oahu | Melvin T. Toma | Severely bitten on right leg by 12-ft tiger shark while swimming at the surface shortly after entering water; site located 300-400 yd from shore over a depth of 20 ft. Looking for fish, but none had been speared when attack occurred; wound required 200 stitches. |
| 70 | 14 Feb. 1982 | White Plains Beach, Barbers Point, Oahu | Lisa Miller | Bitten on left leg while wading in 3 to 4-ft of water; 17 stitches required. |
| 71 | 14 Feb. 1982 | White Plains Beach, Barbers Point, Oahu | Female | Bitten on right foot while swimming in shallow water. |

| Case no. | Date | Location | Victim | Circumstances |
|---|---|---|---|---|
| 72 | 13 June 1982 | Hookipa Beach, Paia, Maui | Scott Shoemaker | Severely bitten three times on the thigh after falling into water while sailboarding 100 yd outside the breakers. Wounds required 120 stitches. |
| 73 | 3 June 1984 | Kaneohe Bay, Oahu | Susan Buecher | Bitten on the foot while towing her sister on a plastic ski board. Incident happened at 5 p.m. in water 5-ft deep, about 400 yd from shore. Surgery and lower leg cast required to repair damaged tendons. 4-5 ft hammerhead shark believed to have been responsible. |
| 74 | 12 Oct. 1985 | Barbers Point, Oahu | Dominic Dela Cruz | Severe gashes to left arm requiring surgery. Attack occurred off Barbers Point Lighthouse while floating on an inner tube after diving for lobster. |
| 75 | 18 Oct. 1985 | Princeville, Kauai | Joe Thompson | Right hand and portion of forearm amputated by a large shark (likely a tiger shark) while body-boarding. Gash sustained to left hand. Right anterior side of board also cut away during same bite by shark. |
| 76*[c] | 20 Apr. 1986 | Kalihiwai, Kauai | Levi Chandler | Fell from rocks and disappeared while fishing at Kalihiwai Point. Pieces of clothing and human flesh were recovered by Fire Department divers who encountered a large shark. |
| 77*[b] | 15 Apr. 1987 | Kailua-Kona, Hawaii | Daniel Kennedy | Last seen swimming from shore out to an anchored sailboat. Swimming trunks found bitten in half on the bottom. |
| 78 | 25 Mar. 1988 | Running Waters Beach, Ninini Point, Kauai | Aaron Kawado | Bitten on the ankle while body surfing in waist-deep water. Surgery required to repair severed vein. |
| 79*[d] | 15 Apr. 1988 | Waihee, Maui | Avery Goo | Lost at sea when the 21-ft powerboat he was on capsized in rough seas. Pieces of human stomach, intestines, and pancreas believed to be from victim found several days later washed ashore along the Waihee shoreline. |

| Case no. | Date | Location | Victim | Circumstances |
|---|---|---|---|---|
| 80*[d] | 8 Jan. 1989 | Wailua, Kauai | Ken Ahlstrand | Disappeared while swimming in strong current with three other people. A 2-day search by helicopters, Civil Air Patrol, and firemen failed to find any trace of the missing man. Lower part of body found 6 days later on 1/14/89 near seawall by the Wailua Golf Course. X-rays of remains revealed teeth marks in femur and tibia. |
| 81 | 20 Jan. 1989 | Waialua Beach, Molokai | Earl Dunnam | Ten-year-old boy bitten on the foot by a 6-8 ft hammerhead shark while riding a body board 200 ft from shore. Wound required 8 stitches. Bite occurred to a naked foot, and not to the foot wearing a swim fin. Note: No known literature documentation. |
| 82 | 3 Apr. 1989 | Hookipa Beach, Paia, Maui | Sam McLain | Sustained a 4-in long crescent-shaped wound on the calf while paddling on a surfboard in whitewater near rocks 50 yards from shore. A sharp "tug" was felt at the time of injury. 13 stitches were used to close the wound. |
| 83 | Apr. 1989 | Kekaha Beach, Kauai | William P. Allen | "Tremendous impact" felt on left leg while paddling on a surfboard in glassy water just beyond swells. Impact lifted board and surfer 2-3 ft out of the water. Left thigh raked with a series of scratches believed to have been caused by teeth. Skegs on the board were knocked loose, and a strip of fiberglass 8-in wide by 5-ft long was torn off. Victim convinced he was attacked by a "huge shark". |
| 84 | 29 June 1989 | Anahola, Kauai | Anthony Paden | Severely bitten on the foot after falling off a surfboard about 20 ft from shore. A "big chunk" taken out of victim's ankle, and "bite marks" inflicted all around the foot. Achilles tendon was half-severed, requiring surgery and a cast. |
| 85*[b] | 14 Oct. 1989 | Kahe Point, Oahu | Ray Mehl, Jr. | Abruptly disappeared while scuba diving as a novice with his partner at a |

| Case no. | Date | Location | Victim | Circumstances |
|---|---|---|---|---|
| | | | | depth of 27 ft, 750 ft from shore near the cooling water discharge pipe of the Kahe Point Power Plant. Unusual behavior exhibited by parrotfish just prior to disappearance. Victim was 10-15 min into the dive with nearly a full tank of air. Dive partner conducted a circle search, but could not locate victim. Time of event was 4:30 p.m., visibility 25-30 ft. Decapitated body with amputated left arm found 200 ft to the west by fire rescue divers the following morning. Large tiger shark suddenly appeared and proceeded to consume rest of body before rescue divers could retrieve it. Small piece of flesh and some dive equipment later recovered. |
| 86*[c] | 12 Nov. 1989 | Ehukai Beach Park, Sunset Beach, Oahu | Edward Malek | Knocked down and swept away by large waves while wading close to shore at 6 p.m. Lower portion of body, sheared at waistline, recovered by fire rescue personnel on the morning of 11/15/89, 1.5 miles to the southwest. Note: The rare sighting of a shark was made at Ehukai Beach Park on 11/5/89, at which time all swimmers were cleared from the ocean for an hour. |
| 87 | 19 Dec. 1989 | 90 miles east of Hilo, Hawaii | George Sohswel | Crew member of the 51-foot fishing vessel One Ki sustained a 23-cm long bite on his left leg and four 7-cm lacerations to left foot. 3 days hospitalization required. Victim transported to Hilo by Coast Guard helicopter. Wound was inflicted by a shark brought aboard the vessel. |
| 88*[b] | 17 Feb. 1990 | Mokapu, Kaneohe Marine Corps Air Station, Oahu | Roy T. Tanaka | Failed to return with his partner (Jake Hernandez) while scuba diving and spearing parrotfish in water 40-ft deep, 200 yards from shore (near firing range) at 9:30 p.m. 22-ft boat nearby had overturned a short time earlier after being hit broadside by a wave. Victim's tank, backpack, dive light, and mask were found on the bottom but not |

| Case no. | Date | Location | Victim | Circumstances |
|---|---|---|---|---|
| | | | | retrieved. Body with amputated right arm sighted from helicopter at 3 p.m. 2/18/90 between Makai Pier and Rabbit Island. Two sharks (8 and 14 ft) seen nearby. Larger shark, apparently reacting to the presence of the helicopter, proceeded to consume all but torso and legs before retrieval. |
| 89 | 1 Apr. 1990 | Silver (Silva) Channels, Waialua Oahu | Everett Peacock | Deep abrasion causing profuse bleeding inflicted to 10-in area on lower left leg while sitting on a surfboard. Also sustained two deep 3-in long gashes above left ankle. Event occurred before 7:30 a.m. in murky water 150 yds from shore. |
| 90 | 3 Apr. 1991 | Oneula Beach Park, Ewa Beach, Oahu | Todd R. Wenke | Bitten on the left leg and foot while sitting on a surfboard 350 yards from shore at 5:30 p.m. at a site known as "Shark Country" 1/4-mile east of Oneula Beach Park. Attack resulted in a 5-in long bone-deep wound on each side of the foot, and a 9-in long bone-deep wound on the calf. 30 stitches, tendon surgery, and a cast required. Only about 18 inches of the shark's head was seen and no positive identification was possible. Shark had "a very large girth." |
| 91 | 26 May 1991 | Maili Beach, Oahu | Frank (Scott) Betz | Bitten on the right calf while sitting on a surfboard 100 yards from shore at 4:45 p.m. Attack resulted in 4-in and a 7-in long wound requiring stitches. Shark estimated to be 8-ft long. Event occurred in murky water. |
| 92*[b] | 19 Nov. 1991 | Maliko Point, Maui | Suk Kyu (Steve) Park | Swept into the sea by a large wave while fishing from the rocky coastline at 4:30 p.m. Victim's son went for help shortly thereafter when it became apparent that surf conditions were too rough for his father to swim ashore. When last seen victim was treading water signaling the son to go for assistance. Help arrived about 30 min later, but no sign of the victim could be found. Victim's shorts |

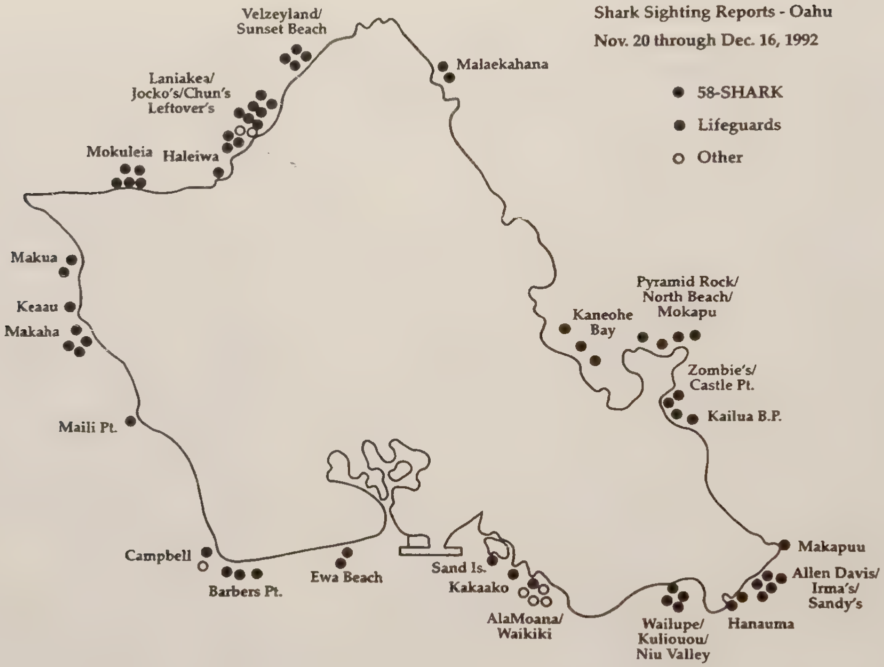
| Case no. | Date | Location | Victim | Circumstances |
|---|---|---|---|---|
| | | | | and shirt were recovered from the ocean bottom the following morning by fire rescue divers. Both garments had large portions missing on the left side. Bite marks present were consistent with attack by a 12-ft tiger shark. Note: Victim was reported to be a strong swimmer in good physical condition. |
| 93*[a] | 26 Nov. 1991 | Olowalu, Maui | Martha J. Morrell | Snorkeling with a female companion at 9 a.m. near reef edge in partly cloudy water 10-15 ft deep about 100 yards from shore, and 50 yards from the end of an old pier next to the victim's beachfront home. An 8- to 11-ft shark passed by the companion and proceeded to attack the victim, initially on the right arm. A small boat was used to recover the body a short time later. Amputations included the victim's right leg at the hip joint, the left leg sheared through the femoral neck, the right forearm, as well as numerous bites and tissue loss elsewhere. |
| 94 | 26 Nov. 1991 | Olowalu, Maui | Louise Sourisseau | Snorkeling companion to Martha J. Morrell (see Case No. 93). Abrasion to right calf when large shark rubbed against her in association with fatal attack on Mrs. Morrell. Following the initial attack on Mrs. Morrell the shark estimated to be 8-11 ft, swam slowly under Louise Sourisseau who assumed a motionless position floating on her back. When first seen prior to the attack, the shark was coming from a seaward direction. No other significant marine life was observed in the vicinity prior to or after the attack. |
| 95*[b] | 19 Feb. 1992 | Leftovers, near Waimea Bay, Oahu | Bryan Adona | Disappeared while body-boarding late in the afternoon at a surfing site about 1.2 mile southwest of Waimea Bay (near 61-350 Kam Highway). The following morning, 2/20/92, his board was found washed ashore at Waimea Bay with a 16-in crescent-shaped piece missing from |

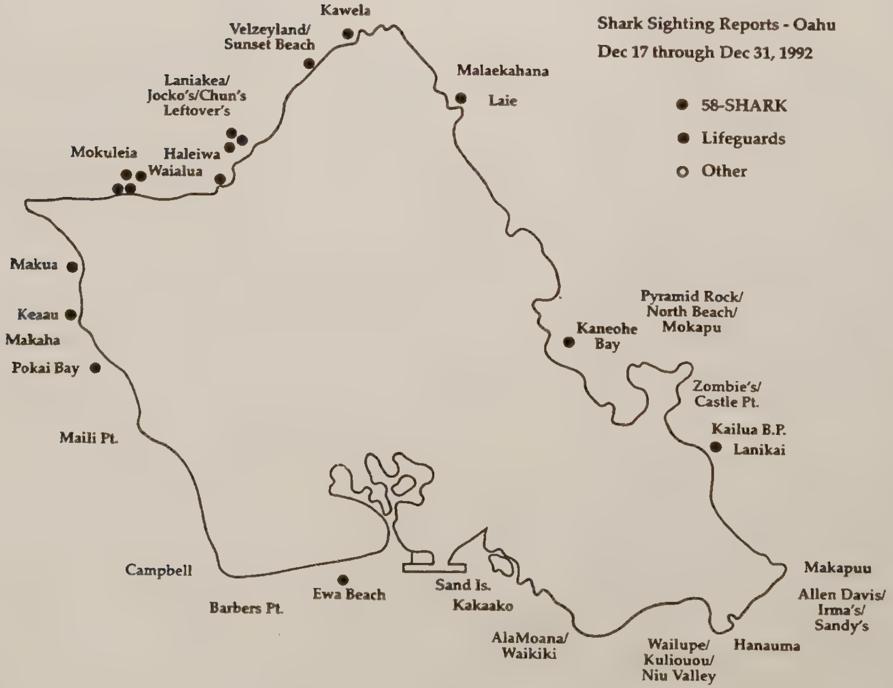
| Case no. | Date | Location | Victim | Circumstances |
|---|---|---|---|---|
| | | | | the anterior left side. Distinct serrations of shark bite were present in board and severed segments of rubber leash still attached to board. Danny Titilah, the last person to see Bryan Adona alive, saw a large shark shortly after he and Adona paddled out toward separate breaks at Leftovers. Others on shore also reported seeing a large shark in the vicinity. Left swim fin, identified as Bryan Adona's, was subsequently found during an extensive search. Strap of fin was severed, but without serrations. |
| 96 | 28 Mar. 1992 | Cannons, Haena, Kauai | Jude Chamberlain | Scratches and small puncture inflicted to foot when a large shark bit her surf board while paddling seaward 10 ft from reef edge (and 85 ft from shore) in clean water about 10 ft deep. 12-14 in. crescent bite marks made in both sides of board. Shark shook board three times then pulled it completely under water and dragged victim by leash for 20 ft before leash severed and shark released surf board. Attack occurred at about 6:45 a.m. after victim had been surfing there for a short time with a friend (Mike Cox), who witnessed the attack at close range. |
| 97*[c] | 23 July 1992 | Waianae, Oahu | Zosimo Popa | Victim and his son (Jeffrey Popa) failed to return from an overnight fishing trip in a 14 ft. boat. Body was found 7/23/92 tied to an ice chest floating 15 miles off the Waianae coast. Victim had sustained two cookie cutter shark bites to the lower back. Wounds were 2 inches in diameter by 1.5 inches deep and were "probably post mortem." Cause of death was "asphyxia by drowning." Life jackets and debris were recovered in the vicinity, but victim's son and the boat were never found. |

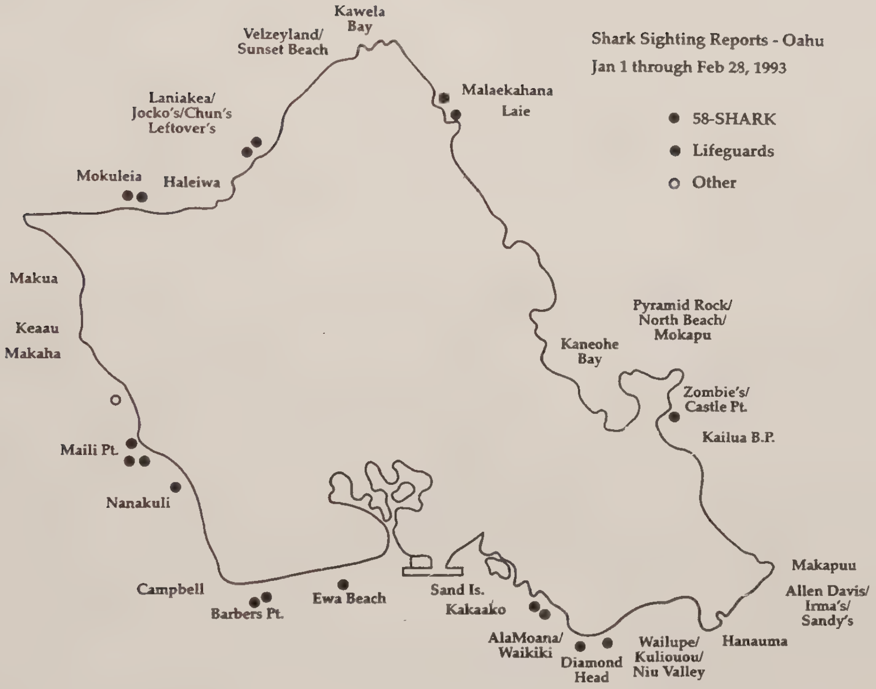
| Case no. | Date | Location | Victim | Circumstances |
|---|---|---|---|---|
| 98*[c] | 21 Aug. 1992 | Twin Arches, Hana Ranch, Maui | Chester N. Shishido | Fell from a cliff while fishing and disappeared in strong current. Rescue efforts were immediately made by the victim's brother and, 30 min. later at 2:30 p.m., by helicopter and a fire rescue unit. No trace of victim was seen and the search was stopped at 5:30 p.m. Body was recovered the following morning (8/22) 200 yards from shore at a depth of 65 ft. Amputations included the left arm, right hand fractured at the wrist, as well as other numerous lacerations and tissue loss consistent with shark bites that "appeared to be post mortem." |
| 99 | 22 Oct. 1992 | Laniakea, Oahu | Eric Gruzinsky | Bruises and scratches to underarm and chest resulting from a 10-12 ft. shark biting a crescent-shaped piece from victim's 6 ft. 4 in. surfboard. Attack occurred at 7:50 a.m. in clear water 15 ft. deep 150 yards from shore. |
| 100*[a] | 5 Nov. 1992 | Keaau Beach Park, Oahu | Aaron A. Romento | Severely bitten in three places on the right leg by a 10-12 ft. shark. Victim was body-boarding at 9:45 a.m. in clear shallow water 30 yards from shore. Death resulted from blood loss and shock a short time after the victim paddled ashore. Wounds did not involve the removal of tissue. |
| 101 | 23 Dec. 1992 | Chun's Reef, Oahu | Gary M. Chun | Cuts to left hand resulting from 10-12 ft. shark biting a 15 in. crescent-shaped piece from victim's surfboard. Attack occurred at 5:30 p.m. while lying on surfboard 100 yards from shore in the presence of 20 or more other surfers. Victim was surfing "near a channel where the current flows like a river through a break in the reef." |
| 102 | 28 Dec. 1992 | Honomuni, Molokai | Pahu Tanaka | Abrasion and bruise to right leg of 10-year old boy inflicted by 8-ft tiger shark. Victim was standing 50 yards from shore in waist-deep water in the morning helping his father tend a gill net containing dead fish. |

| Case no. | Date | Location | Victim | Circumstances |
|---|---|---|---|---|
| 103 | 14 Mar. 1993 | Wailuaiki Bay, Maui | Roddy P. Lewis | Severely bitten on the legs by a 12-14 ft. shark while paddling on a 7 ft. 4 in. surfboard at 3:45 p.m. about 100 feet from shore near a river mouth. Shark shook victim but let him go after he punched it on the side of the head. Victim's lower right leg sustained a 14.5 in. gaping cut on the inside, and a 13 in. one on the outside, requiring 145 staples and an unknown number of internal sutures. Left leg sustained a 4 in. cut needing 7 staples. Five separate surgeries were needed to repair tissue damage. Fragment of tiger shark tooth removed from victim's leg bone. Only two other surfers were in the vicinity when the attack occurred. Water visibility estimated to be 5 feet. |
| 104 | 10 June 1993 | Malaekahana State Recreation Area, Laie, Oahu | Jonathan Mozo | Bitten on the feet while paddling on a 6 ft. surfboard in shallow water at 7:10 a.m. 100 yards from Goat Island (Mokuauia). When attack occurred, victim looked back and saw a large shark with its mouth wide open. Victim raised up his legs and paddled to shore as fast as possible. Numerous lacerations sustained requiring 30 stitches to each foot. Victim's companion (Ryan Bell) was on a body board nearby and felt something bump him shortly before the attack. Victim and companion were the only people in the water at the time. |

# APPENDIX B
# MAPS OF SHARK SIGHTINGS AND TIGER SHARK REMOVALS


Shark Sighting Reports - Oahu
Nov. 20 through Dec. 16, 1992
● 58-SHARK
● Lifeguards
○ Other
Velzeyland/ Sunset Beach
Malaekahana
Laniakea/ Jocko's/Chun's Leftover's
Mokuleia
Haleiwa
Makua
Keaau
Makaha
Maili Pt.
Kaneohe Bay
Pyramid Rock/ North Beach/ Mokapu
Zombie's/ Castle Pt.
Kailua B.P.
Makapuu
Allen Davis/ Irma's/ Sandy's
Hanauma
Wailupe/ Kuliouou/ Niu Valley
AlaMoana/ Waikiki
Kakaako
Sand Is.
Ewa Beach
Barbers Pt.
Campbell


Shark Sighting Reports - Oahu
Dec 17 through Dec 31, 1992
● 58-SHARK
● Lifeguards
○ Other
Kawela
Velzeyland/ Sunset Beach
Malaekahana
Laie
Laniakea/ Jocko's/Chun's Leftover's
Mokuleia
Haleiwa
Waialua
Makua
Keaau
Makaha
Pokai Bay
Maili Pt.
Kaneohe Bay
Pyramid Rock/ North Beach/ Mokapu
Zombie's/ Castle Pt.
Kailua B.P.
Lanikai
Makapuu
Allen Davis/ Irma's/ Sandy's
Hanauma
Wailupe/ Kuliouou/ Niu Valley
AlaMoana/ Waikiki
Kakaako
Sand Is.
Ewa Beach
Barbers Pt.
Campbell



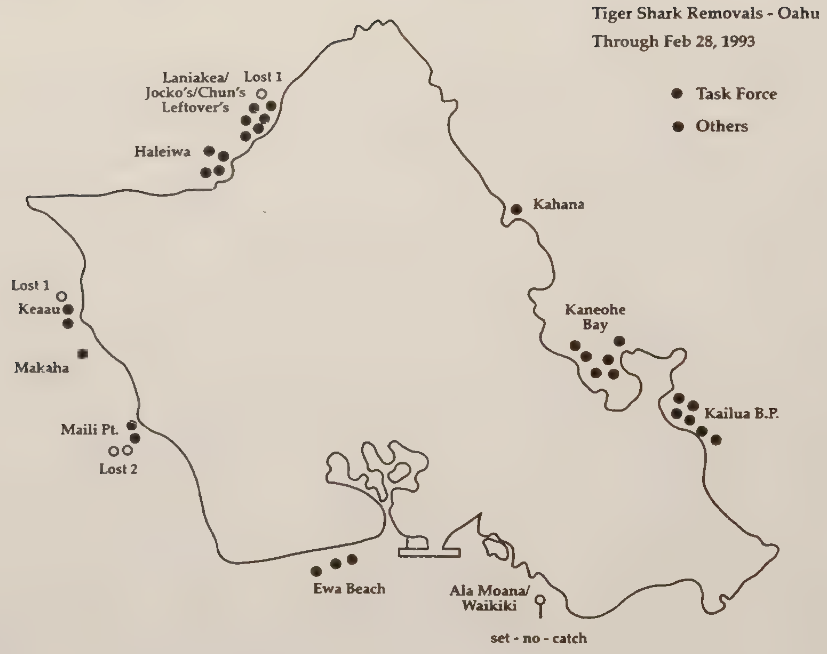
Shark Sighting Reports - Oahu

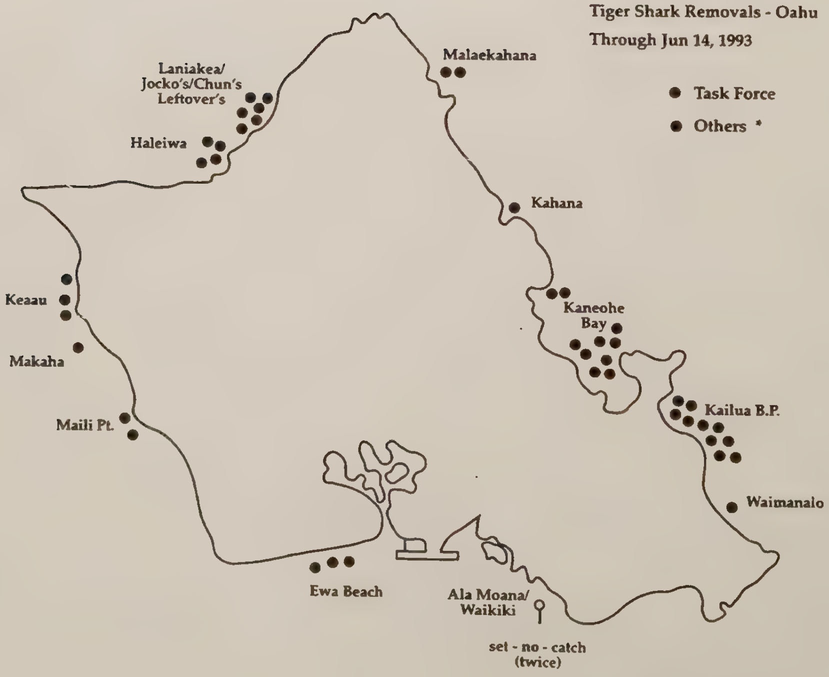
Jan 1 through Feb 28, 1993

● 58-SHARK
● Lifeguards
○ Other
Kawela Bay
Velzeyland/ Sunset Beach
Malaekahana
Laie
Laniakea/ Jocko's/Chun's Leftover's
Mokuleia
Haleiwa
Makua
Keaau
Makaha
Pyramid Rock/ North Beach/ Mokapu
Kaneohe Bay
Zombie's/ Castle Pt.
Kailua B.P.
Maili Pt.
Nanakuli
Makapuu
Allen Davis/ Irma's/ Sandy's
Campbell
Barbers Pt.
Ewa Beach
Sand Is.
Kakaako
AlaMoana/ Waikiki
Diamond Head
Wailupe/ Kuliouou/ Niu Valley
Hanauma

Source: Department of Land and Natural Resources

## SHARK REMOVAL AREAS


Tiger Shark Removals - Oahu
Through Feb 28, 1993
● Task Force
● Others
Laniakea/
Jocko's/Chun's
Leftover's
Lost 1
Haleiwa
Kahana
Lost 1
Keaau
Makaha
Kaneohe
Bay
Kailua B.P.
Maili Pt.
Lost 2
Ewa Beach
Ala Moana/
Waikiki
set - no - catch


Tiger Shark Removals - Oahu
Through Jun 14, 1993
● Task Force
● Others *
Malaekahana
Laniakea/
Jocko's/Chun's
Leftover's
Haleiwa
Kahana
Keaau
Makaha
Kaneohe
Bay
Kailua B.P.
Maili Pt.
Waimanalo
Ewa Beach
Ala Moana/
Waikiki
set - no - catch
(twice)

* Waikiki catches by
Kamisugi not included

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# Marine Turtle Faeces on Hawaiian Beaches

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**Faeces of the green turtle, *Chelonia mydas*, washed ashore in large numbers at a beach park in Hawaii over a 40-day period in 1989. The formed pellets were originally misidentified as being from pigs or humans, and therefore were perceived as a pollutant of potential health hazard to humans. However, bacteriological analysis of the nearshore waters indicated low and legally acceptable levels of faecal coliforms and enterococci. Similar diminished levels were also found in direct cultures of the fresh pellets. Green turtle faeces have been known to drift ashore in Hawaii, but never in the quantities recorded during this short-term event. The reason for the occurrence could not be determined, but several possible explanations are given.**

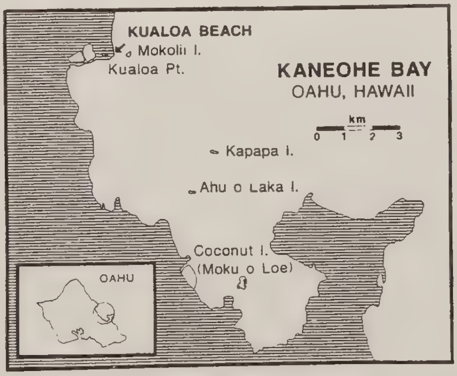

**Fig. 1** Location of Kualoa Beach (21°31′N, 158°51′W) where faeces of the green turtle washed ashore in record numbers during 1989. Kaneohe Bay, the largest bay in the Hawaiian Islands, is 13 km long and 4 km wide.

During July of 1989, numerous floating faecal pellets began to wash ashore on the island of Oahu at Kualoa Beach Park located at the northwestern end of Kaneohe Bay, the largest bay in the Hawaiian Islands (Fig. 1). As a precautionary measure, the State of Hawaii's Department of Health closed this 1 km stretch of beach to public use. At the same time an effort was made to determine the source of the pellets and their possible health hazards. Sewage spills into Hawaii's nearshore waters from treatment plants have been reported but have never resulted in the appearance of formed faeces in the water. No spills of this nature occurred at the time. Faecal wastes from domestic pigs being transported by barge were initially suspected. The possibility of a human origin from tourist-related recreational activities was also suggested by the news media, but this was unlikely. Coliform counts in surrounding waters, however, were not elevated (Fig. 2) as might be expected in such cases.

A more careful investigation of the droppings revealed them to be faeces originating from the herbivorous green turtle, *Chelonia mydas*. The pellets ranged from 0.5 to 2 cm in diameter and up to 5 cm long (Fig. 3). They were found to consist almost entirely of partially digested benthic algae, mainly *Codium edule* and *Amansia glomerata*, which are commonly eaten by green turtles in Hawaii. Algal particles were clearly discernible with the naked eye after the pellets were broken open. In addition, ova in the faeces were determined to be from non-mammalian parasites, and most likely from flukes that parasitize green turtles in Hawaii (Dailey *et al.*, 1991). The pellets were green to brownish in colour and 'dog-like' in appearance. They had a distinctly different and somewhat less objectionable odour than mammalian faeces, and appeared to be less attractive to flies and other insects.

Kualoa Beach was reopened after a 40-day closure (11 August–22 September 1989) when the daily number of pellets declined and any health risks to humans were judged to be minimal (Fig. 4). During the

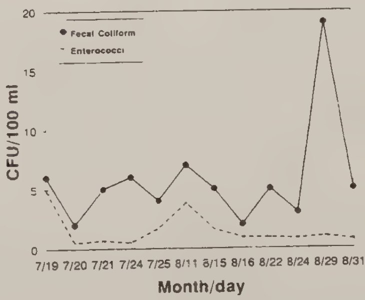

**Fig. 2** Faecal coliform and enterococci counts (Colony Forming Units (CFU) per 100 ml) in the nearshore waters at Kualoa Beach, 19 July to 31 August, 1989, sampled while green turtle pellets were washing ashore.

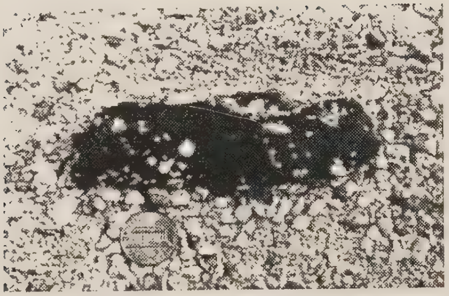

Fig. 3 Faecal pellet of a green turtle washed ashore at Kualoa Beach.

periods of greatest abundance, over 300 pellets per day (maximum 470 pellets) were counted and picked up for disposal by park maintenance personnel. A total of nearly 5500 pellets were removed during the 40 days. Even after the beach was reopened, pellets continued to float ashore, but in much reduced numbers.

## Bacteriological Analyses

Despite the high abundance of faecal pellets seen during the 40 days, nearshore water samples analysed by the Department of Health did not exceed indicator bacterial limits set by the US Environmental Protection Agency for ocean recreational waters (i.e. <33 Colony Forming Units of faecal enterococci per 100 ml of sea water, Fig. 2). Spills from sewage treatment plants have on occasion produced counts in Kaneohe Bay of up to 2300 CFU of faecal coliform and 570 CFU of enterococci (State of Hawaii, Department of Health, pers. comm.).

To measure bacteriological aspects of the turtle faeces, a preliminary follow-up study was conducted. Faecal coliforms and faecal enterococci from turtle pellets freshly collected at Kualoa were found to be low (most probable number (MPN) 3–43 $g^{-1}$ of faeces), compared with mammalian and avian faeces (MPN $10^6$–$10^8$ $g^{-1}$ of faeces). Furthermore, turtle pellets held at laboratory room temperature (21.5–25.5°C) showed no multiplication of faecal coliforms or enterococci. Pellets placed in beakers of seawater for 15 days continued to remain intact, and mostly buoyant, with no bacterial growth. Breaking the faeces into small pieces after 15 days failed to result in the isolation of faecal coliforms or enterococci (Fujioka, 1990). Cultures from fresh pellets performed by a private hospital laboratory, as well as the State of Hawaii's Department of Agriculture, were found to be negative for Salmonella.

## Results and Discussion

Faecal pellets of the green turtle have been known since 1976 to occasionally wash ashore in small numbers on certain beaches throughout the Hawaiian Islands. The opportunity to easily collect this material has provided a simple method of identifying food sources exploited by the turtles in their nearshore foraging pastures (Balazs, 1980). However, Kualoa is not a site where this phenomenon had been previously reported. Park maintenance personnel, lifeguards, and other people long familiar with Kualoa Beach unanimously agreed that large numbers of faeces have never washed ashore there.

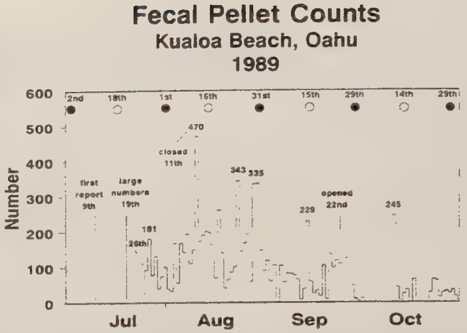

Fig. 4 Green turtle faecal pellet counts at Kualoa Beach, July–October 1989. The State of Hawaii's Department of Health closed the beach to public use from 11 August–22 September, 1989.

No unusual seasonal weather conditions, nor notable activity by turtles immediately off Kualoa, occurred that might explain the observed faecal event. A general review of data for tidal cycles, moon phases, wind speed and direction, and surf conditions failed to identify any consistent correlation with the erratic fluctuations in daily faecal counts recorded (Fig. 4). Southeasterly winds prevailed on 28–29 August 1989, which partly coincided with counts of 335 pellets per day ashore for 2 days in a row. However, no such relationship was apparent for any of the other days studied. It should be noted that green turtles are only occasionally sighted directly off Kualoa, where they sometimes become entangled in fishing lines or wash ashore dead from various causes.

The most plausible area for the faecal pellets to have originated appears to be Kaneohe Bay, which extends for some 13 km immediately to the southeast of Kualoa Beach (Fig. 1). A comparatively large aggregation of green turtles, estimated at 500 or more individuals mainly composed of immature size classes resides in this bay for foraging and resting purposes. There is no evidence that a sudden increase in turtles occurred during 1989 (or in any other year). However, for the past 4 years, special attention has been focused on the turtles in Kaneohe Bay because of the documented increased incidence of fibropapillomas, a debilitating and life threatening tumour disease of unknown aetiology. About 50% of all green turtles found washed ashore in a dead or disabled condition in the Hawaiian Islands have these tumours (Balazs & Pooley, 1991). In addition, about half of the turtles sighted during diving surveys in Kaneohe Bay now have these tumours to varying degrees of severity.

The possibility exists that the large quantity of faeces that washed up on Kualoa Beach during the summer of 1989 may have been related in some way to the tumour epidemic in Kaneohe Bay. However, the manner in which this might have been mediated remains unknown.

and open to speculation. Perhaps a sudden surge of the disease reduced the turtles' ability to adequately digest algae, possibly by changes in intestinal microbes, thereby causing the faecal pellets to be more buoyant and resistant to breakdown. It is known that many, and possibly most, faecal pellets from Hawaiian green turtles are not buoyant but rather sink to the bottom, and hence never wash ashore.

Another hypothesis is that certain turtles feeding exclusively on *Halophila hawaiiana*, a sea grass that grows in Kaneohe Bay, moved to algal foraging habitats during the summer of 1989. Bjorndal (1980) has pointed out that a change of diet by the green turtle, from sea grass to one of algae, would likely require radical changes in intestinal microflora resulting in a lowered digestive efficiency, at least for a period of time. Such a move could have been related to the tumours and/or the considerable increase in commercial tourist-related activities and associated disturbances to foraging turtles in the bay. Since 1989, certain sections of Kaneohe Bay where turtles forage heavily on *Halophila* have been legally set aside as zones that exclude anchoring by commercial tour operators.

Kualoa Beach has been periodically monitored for a reoccurrence of the mass arrival of faecal pellets since late 1989. Such an event has not been seen again, although small numbers continue to wash ashore both at Kualoa and elsewhere in Hawaii. Even at low levels, the drifting ashore of these faeces appears to be unique. No other published or even anecdotal reports are known of faecal pellets of the green turtle, or any other species of marine turtle, washing up at any location outside of the Hawaiian Islands.

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# AN EXPERIMENTAL AERIAL SURVEY FOR VAQUITA (*PHOCOENA SINUS*) IN THE NORTHERN GULF OF CALIFORNIA, MEXICO

The vaquita (*Phocoena sinus*) is endemic to the Gulf of California and all recent sightings have been in the northern Gulf (Silber 1990*a, b*) where most survey efforts for this species have been concentrated. Previous ship surveys for this species were conducted by Villa-R. (1976), Wells *et al.* (1981), Vidal *et al.* (1987), and Silber (1990*b*) (Table 1). Aerial surveys were also conducted by Silber (1990*b*) and Silber and Norris (1991). None of these surveys produced quantitative estimates of vaquita population size. We conducted an experimental aerial survey in the northern Gulf of California from 11 to 14 September 1991 to evaluate the feasibility of using aerial census methods to estimate vaquita population size.

The line-transect methods and aircraft used in this experimental work were the same as were used in quantitative surveys of harbor porpoise (*Phocoena phocoena*) in California (Forney *et al.* 1991). The aircraft was a twin-engine Partenavia P-68 fitted with bubble windows on each side and a 20 × 30-cm viewing port in the belly of the aircraft. Direct downward visibility was possible from all three observer positions. Surveys were flown at an airspeed of 166 km/h and an altitude of 183 m. Transects were established on a uniform grid at 22.2 km spacing (Fig. 1). The starting point of the grid was chosen arbitrarily as the intersection of latitude 30°45′N with the eastern shoreline of the Gulf. The initial survey design included only areas north of 30°45′N (which enclosed the area of all confirmed sightings reported by Silber [1990*b*]). Survey lines were added in shallow waters immediately south of the primary grid along the western shoreline of the Gulf after hearing a report by local fishermen of vaquita

*Table 1.* Scientifically documented sighting history for vaquitas in the Gulf of California. Effort indicates the number of transect km surveyed (by boat unless noted otherwise). Caveats on identification expressed by the author are given below the source citation.

| Date | Effort | Number sightings | Number individuals | Approximate location | Source |
|---|---|---|---|---|---|
| Jan 1951 | — | 1 | 2 | Topolobampa | Norris and McFarland (1958)<br>(identification doubtful) |
| Feb 1953 | — | 1 | 1 | San Carlos | Norris and McFarland (1958)<br>(identification doubtful) |
| Apr 1955 | — | 1 | 3 | San Felipe | Norris and McFarland (1958) |
| Feb 1956 | — | 1 | "large group" | Conception Bay | Norris and McFarland (1958) |
| May 1956 | — | 1 | 1 | Bacochibampo Bay | Norris and McFarland (1958)<br>(identification probable) |
| Apr–May 1976 | 720 km | 3 | 5 | San Francisquito Bay | Villa-R. (1976) |
| Mar 1981 | 1,959 km | 2 | 5 | Puerto Peñasco | Wells *et al.* (1981) |
| Spring 1984 | 1,665 km | 1 | 1 | — | Vidal *et al.* (1987) |
| 1985–1986 | — | 20 | — | — | Pérez-D. (1987) |
| 1986 | 300 km | 1 | 1 | Santa Clara | Turk *et al.* (1986) |
| Feb–Mar 1986 | 815 km | 12 | 27 | San Felipe | Silber (1987) |
| Apr–May 1987 | 300 km | 22 | 46 | San Felipe | Silber (1987) |
| Mar–May 1988 | 130 km | 8 | 12 | San Felipe | Silber (1990*a*) |
| May 1988 | 1,521 km aircraft | 5 | 11 | San Felipe | Silber (1990*a*) |
| Sep 1989 | 980 km aircraft | 7 | 14 | San Felipe | Silber and Norris (1991) |
| Sep 1991 | 1,143 km aircraft | 1 | 2 | Puertecitos | this paper |

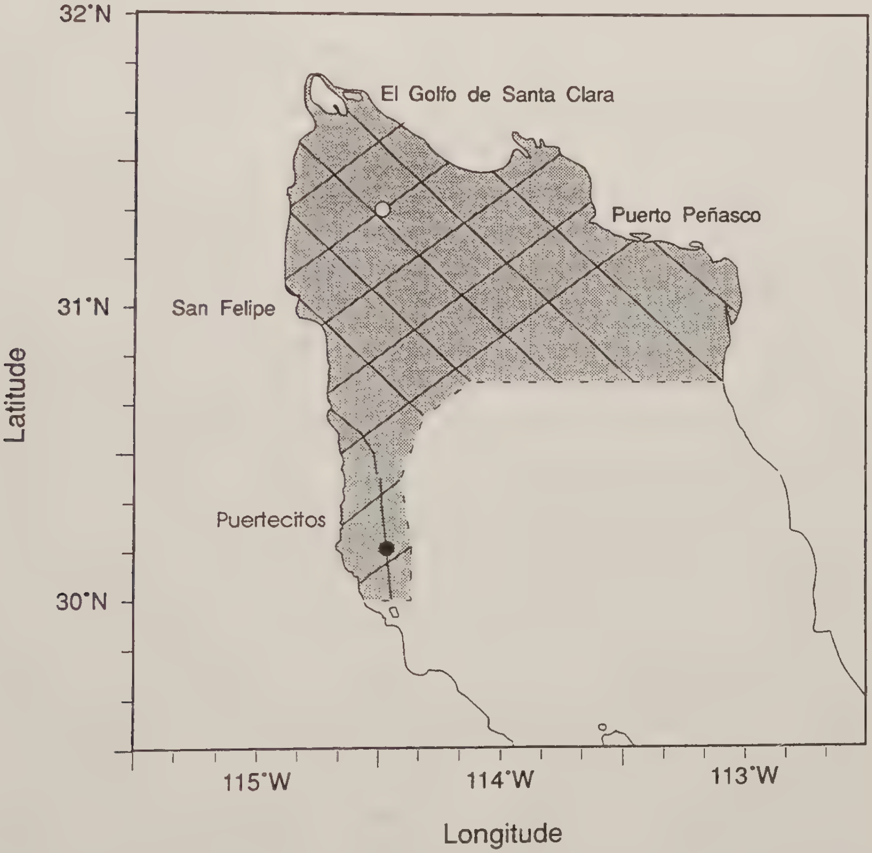

*Figure 1.* Survey transect lines flown in the northern Gulf of California during the experimental aerial survey for vaquitas. The lower (southernmost) solid circle indicates the position of the only confirmed sighting of vaquitas. The upper open circle indicates the position of a probable sighting.

being in that area in September. All transects were flown towards the northwest in the mornings and towards the northeast in the afternoons to minimize sun glare. Observers consisted of the four authors, who rotated among four positions. Two of the observers (J.B. and K.A.F.) have extensive experience (>3 yr) conducting similar aerial surveys for *Phocoena phocoena*. The primary observer team consisted of left (seated behind pilot), right (seated behind recorder), and belly (lying down in rear of aircraft and viewing through the belly port) positions. The fourth position was data recorder (in the co-pilot seat). The pilot and data recorder were instructed not to mention cetacean sightings until after they had passed out of the field of view of the primary observation team. The perpendicular distance from the transect line to any observed marine mammal was calculated from altitude and declination angle measured using hand-held clinometers. The width of the search path was unbounded, but observers were told to concentrate their efforts close to the trackline. Information on changes in sea state and viewing conditions were recorded immediately on a lap-top computer which was linked to aerial navigation instruments. Position was determined by LORAN which had been calibrated using a GPS satellite navigation device.

A total of 1,143 km was completed on aerial transect lines during 3.5 d of surveying. Two transect lines in the southeast (not shown in Fig. 1) were not completed due to insufficient time. All transects were completed under clear skies and with Beaufort sea state conditions of 0–1 (155 km), 2 (503 km), 3 (472 km), or 4 (13 km). Only one sighting of two vaquita was made by the primary survey team. Another probable sighting of one vaquita was made by the data recorder. [Sightings made by the data recorder are typically not used in harbor porpoise population estimates because the fraction of time they are actively searching is difficult to quantify (Barlow *et al.* 1988).] Other species seen included common dolphins (*Delphinus delphis*), bottlenose dolphins (*Tursiops truncatus*), false killer whales (*Pseudorca crassidens*), fin whales (*Balaenoptera physalus*), minke whales (*Balaenoptera acutorostrata*), and California sea lions (*Zalophus californianus*).

The only certain vaquita sighting was made south of San Felipe, Baja California Norte, under clear skies, with Beaufort 1, and in relatively clear waters (Fig. 1). Two vaquitas were traveling rapidly approximately 2 m under the surface, breathing relatively infrequently in the characteristic "pop-splash" of rapidly moving harbor porpoise (Taylor and Dawson 1984). All observers obtained a good view of these animals while the aircraft circled. The other, "probable" sighting occurred in the region north of Rocas Consag where vaquitas have been most frequently reported (Silber 1990*b*) (Fig. 1). That sighting occurred in very turbid waters by only one person for less than 1 sec. The animal surfaced once and dived straight down, disappearing within 1 m of the surface due to the turbid conditions. Based on extensive experience on harbor porpoise aerial surveys, the data recorder (K.A.F.) classified that animal as a probable *Phocoena*.

Clearly, insufficient sightings were made to make a reliable line-transect estimate of vaquita population size from this survey. However, it is clear that vaquita were relatively scarce in our study area. Both *Tursiops* and *Delphinus* were seen more frequently. The sighting rate for vaquitas was 1.8 per 1,000 linear km surveyed (or 2.6 per 1,000 km including the "probable" sighting). This is lower than sighting rates on previous aerial surveys which concentrated effort in areas of presumed high density: 7.2 vaquitas per 1,000 km (Silber 1990*b*) and 7.0 per 1,000 km (Silber and Norris 1991). In contrast, 47.0 harbor porpoise per 1,000 km were seen on systematic aerial surveys in central California (Forney *et al.* 1991).

Although this study and others (Silber 1990*b*, Silber and Norris 1991) have shown that vaquitas can be seen from aircraft, quantitative aerial surveys for this species are plagued by difficulties and uncertainties. From the sighting rate of this survey, it is clear that a much larger-scale survey is needed for reliable population estimates. A sample size of 100 sightings is desirable to allow stratification by Beaufort sea state and cloud cover, factors that have been shown to be important in harbor porpoise aerial surveys (Forney *et al.* 1991). This would require a great amount of effort, and a synoptic survey of this magnitude would require the coordinated work of several aircraft. Another major impediment is the difficulty in quantifying the fraction of animals that are visible from the air. A simple line transect estimate only represents the number visible from the air at any given moment. For harbor porpoise seen in relatively clear waters in California, a correction factor of 3.2 has been used to account for submerged animals that would not be visible from the air (Barlow *et al.* 1988). A correction factor for submerged animals is likely to depend on water turbidity. Turbidity in the northern Gulf of California is typically much greater than in California and is influenced by tides and by sediment transport from the Colorado River. Turbidity in the Gulf changes markedly over very short distances. Not only would several correction factors be needed for different water turbidities, but also some method would be needed to accurately quantify turbidity during aerial surveys. Uncertainty in estimating these (probably large) correction factors would add considerable uncertainty to quantitative estimates of population size. Future aerial surveys should be preceded by studies of the fraction of time vaquitas are visible from the air, perhaps using the type of helicopter experiment that was used to obtain these data for harbor porpoise (Barlow *et al.* 1988).

Turbidity and fraction of time spent at the surface are less of a problem for ship than for aerial surveys. Although cetaceans are typically seen from ships only when some part of the animal is above the surface, surface vessels travel relatively slowly and most animals will surface at least once within the visual range of the ship. Given the difficulty and uncertainty in estimating the large correction factors for submerged animals on aerial surveys, effort might be better allocated to large-scale ship surveys.

## Acknowledgments

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# Estimated drift gillnet selectivity for albacore *Thunnus alalunga*

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Drift gillnet (DGN) fisheries, some directed toward albacore *Thunnus alalunga* and some toward other species, have operated in the north and south Pacific Ocean. These fisheries, some of which had their beginnings decades ago, expanded in the early 1980s and exerted a substantial, but as yet unknown, mortality on Pacific albacore populations. Knowledge of the selectivity of DGNs is useful for applying complex population-dynamics techniques to the albacore population.

Several DGN experimental surveys conducted in the north and south Pacific Ocean have produced data on albacore distribution and gear selectivity. In 1984–85 the Southwest Fisheries Science Center of the National Marine Fisheries Service (NMFS) undertook an experiment to quantify DGN mesh-size selectivity for albacore. The experiment produced size-selectivity data for a single mesh size used in the U.S. DGN commercial fishery for albacore (184 mm; all mesh sizes referred to are stretch mesh measurements), in the eastern North Pacific Ocean. Other experiments designed to sample albacore were conducted by the Japan Marine Fishery Resource Center in 1980 (JAMARC 1983), 1982 (JAMARC 1985), and 1983 (JAMARC 1986). These experiments used other mesh sizes which produced complimentary data used in this study. The objective of this analysis was to quantify drift gillnet mesh-size selectivity for albacore, using existing data collected from various experiments and surveys in the Pacific Ocean.

## Methods

Various experiments providing data have been conducted independently at different times and in different areas (Fig. 1). Consequently, some assumptions had to be made concerning comparability of nets used and availability and vulnerability of fish sizes to be sampled. However, there was enough information to provide insights into net selectivity for albacore. The nets used in all the experiments were similar to typical Japanese commercial drift nets. All nets had similar mesh-hanging ratios, twine/mesh-size ratios, and were of multifilament construction (Table 1). These are the most important factors affecting the selectivity curve for a given mesh size (Hamley 1975).

Detailed descriptions for the JAMARC experiments, including set locations, timing, mesh size placement, etc, are contained in the JAMARC references. These experiments were designed to obtain information on resource distribution and catch rates for possible future commercial fisheries. In brief, the JAMARC North Pacific experiment was a 1yr survey beginning in the spring of 1980 (Fig. 1). It targeted albacore using nets with mesh sizes of 130–250mm. The JAMARC 1982 and 1983 experiments in the South Pacific were conducted in the area shown in Fig. 1 and targeted all tuna-like species, using 180 mm mesh nets in 1982, and 118 mm and 160–180 mm mesh nets in 1983.

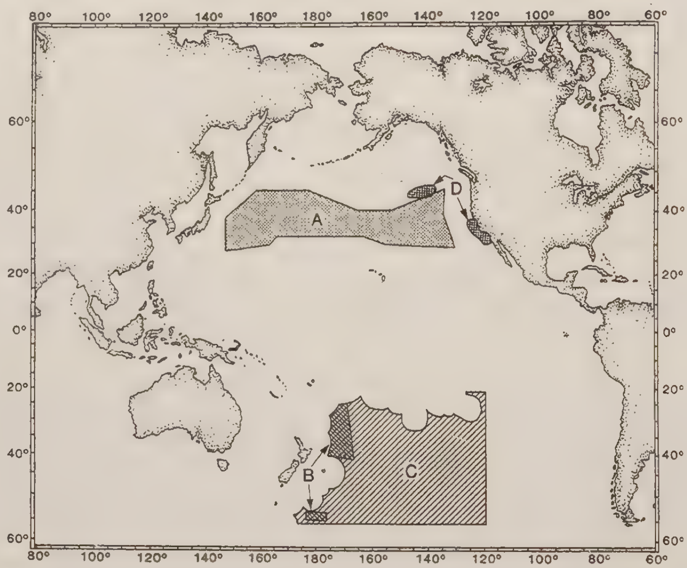
The NMFS experiment targeted albacore. A total of 27 night sets was made: 12 sets in waters south of Point Conception and within 300 mi of shore; 7 sets in the vicinity of the Guide Seamount south of the Farallon Islands; and 8 sets approximately 1000 mi west of Oregon near 142°W long. and 45°N lat. (Fig. 1). All sets used 184 mm mesh nets.

In all the experiments using mesh sizes of >130 mm, the amount of gear fished during each set ranged from 2760 m to 10,800 m, and the number of sets ranged from 11 to 176 (Table 1). Nets in each experiment were deployed and retrieved as in typical commercial operations. Nets were deployed at dusk, and retrieval began at first light often extending into midmorning. Soak times were ~10–16 h/set.

## Data collected

Data published by JAMARC are limited to fork length (FL) frequencies by mesh size by set. The NMFS data include fork length-frequencies, maximum or largest body girth, and opercular girths for each fish, and notation on the mode of capture for each fish (tangled, wedged, or gilled). Fish were described as wedged or gilled when inserted into a mesh so that the entire perimeter of the mesh held the fish. This occurred at locations on the body from the snout to the point of maximum body girth. Fish were described as tangled when snared or tangled by fins or tail. Length-frequencies for U.S. troll-caught fish from the same time and areas are available for

Manuscript accepted 9 February 1993.
Fishery Bulletin, U.S. 92:371-378 (1993).



### Figure 1

Areas sampled for albacore *Thunnus alalunga* by drift gillnets. **(A)** JAMARC 1980 survey (JAMARC 1983); **(B)** JAMARC 1982 survey (JAMARC 1985); **(C)** JAMARC 1983 survey (JAMARC 1986); **(D)** NMFS 1985 experiment.

### Table 1

Characteristics of drift gillnets used, amount of gear fished, and alalunga caught for selected stretch mesh sizes.

| Survey | Mesh size | Twine size (dinier/strand) | Net material | Hang-in-ratio (% stretch mesh Distance/hanging) | No. set |
|---|---|---|---|---|---|
| JAMARC 1980 | 130 | 210/21 | Nylon | 56.1 | |
| (JAMARC 1983) | 150 | 210/24 | Nylon | 56.1 | |
| North Pacific | 160 | 210/27 | Nylon | 56.1 | |
| | 170 | 210/30 | Nylon | 55.5 | |
| | 180 | 210/33 | Nylon | 56.1 | |
| | 200 | 210/36 | Nylon | 56.1 | |
| | All | | | | 178 |
| JAMARC 1982<br>(JAMARC 1985)<br>South Pacific | 180 | 210/30 | Nylon | 55.3 | 38 |
| JAMARC 1983<br>(JAMARC 1986)<br>South Pacific | 118 | 210/10 | Nylon | | 11 |
| NMFS 1985<br>North Pacific | 184 | 210/18 | Polyester | 50.0 | 27 |

comparison. Sample sizes of albacore caught by mesh size for each experiment, as well as the quantity of gear fished, are shown in Table 1.

## Results

### JAMARC 1980 data

Gear selectivity can only be estimated because there is no information on the actual size structure of the North Pacific albacore population (Hamley 1975). Data from several mesh sizes fished simultaneously and assumptions about shape, variance, and efficiency of the selectivity curves are required. The JAMARC 1980 experiment provided the only published dataset containing this information. Length-frequencies obtained in the 1980 experiment for mesh sizes 130, 150, 160, 170, 180, and 200 mm are shown in Fig. 2 (A–F). In all these mesh sizes, albacore captured had size modes at 53, 62, and 78 cmFL.

Two options are available for calculating an indirect selectivity curve: (1) Fitting a predetermined distribution function to data, using a method similar to that of Ishida (1962); or (2) estimating the selectivity of different meshes to one common size-class (mode) of fish and extrapolating to other mesh sizes (Regier & Robson 1966). Lack of an objective mathematical function in determining the shape of the selectivity curve in the first method, and the need for fitting the selectivity curve "by eye," required that a combination approach was employed.

A basic assumption of gillnet selectivity analysis is that selectivity is the same for those combinations of length interval L(i) and mesh size M(j) where the ratios of L(i)/M(j) are equal (Regier

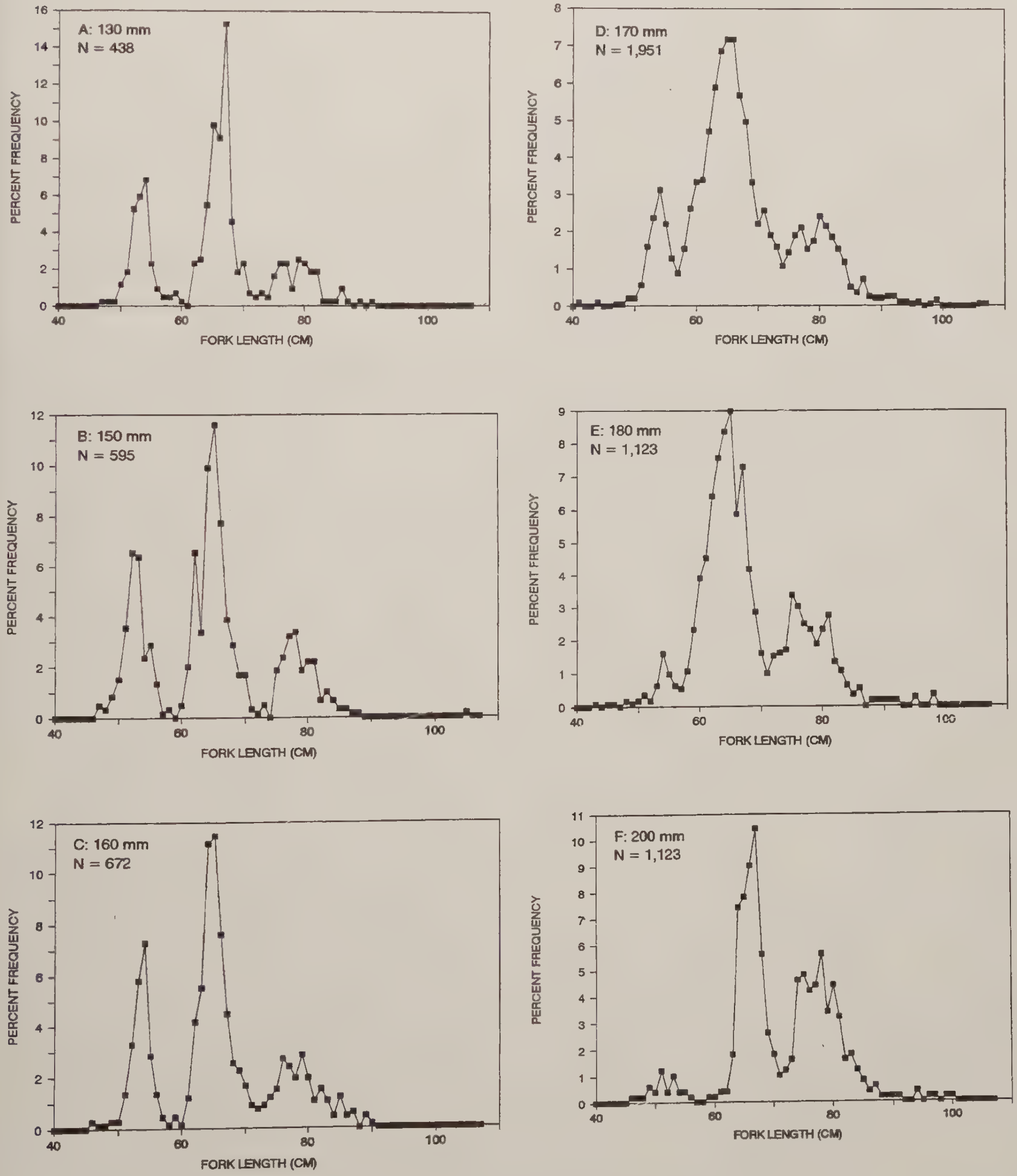


**Figure 2**

Percent frequency-of-occurrence of albacore *Thunnus alalunga* by fork-length interval by stretch-mesh size. Data from the 1980 JAMARC survey (JAMARC 1983). **(A)** 130mm mesh; **(B)** 150mm mesh; **(C)** 160mm mesh; **(D)** 170mm mesh; **(E)** 180mm mesh; **(F)** 200mm mesh.

& Robson 1966). This assumes that the length:girth ratio is the same for all fish. Each fork-length interval was divided by the appropriate mesh size of capture, and then multiplied by the appropriate observed frequency. This produced "generic" size-frequencies by mesh size. Each resulting size-frequency interval, by mesh size, was normalized to the greatest frequency. The resulting frequencies, one for each mesh size, were then scaled to an assumed 100% efficiency at the peak frequency sampled (the mid-60 cm mode); thus, differential sample sizes by mesh are taken into account. If all mesh sizes have the same selectivity curve, and no sampling variance, they would all be the same.

Rather than using the method of Ishida to describe a common selectivity curve (Regier & Robson 1966), the "mean" shape of the selectivity curve was estimated from the selectivity of the different mesh sizes for the largest (78 cmFL) and smallest (53 cmFL) modes captured by all mesh sizes. The curve obtained for the 53 cm mode described the left or ascending limb of the selectivity curve, and the curve for the 78 cm mode described the right or descending limb. Lengths between these two limbs were assumed to be sampled at 100%. This included some lengths with very low percent-frequencies (i.e., we assumed few fish were available) as well as the size mode near 62 cm. There was no assumption that the left and right limbs have the same shape.

For the 78 cm mode, the cumulative percent-frequency of capture vs. length of fish caught for all mesh sizes are shown in Fig. 3. When plotted on normal probability scales, cumulative percent-frequencies formed straight lines with virtually the same slopes. An average cumulative percent-frequency (subtracted from 100) provided the shape of the right limb (Fig. 4). This introduced the assumption of a constant variance and normal distribution (Hamley 1975). The same procedure provided the left limb of the selectivity curve which increased more rapidly or had a greater slope (Fig. 5).

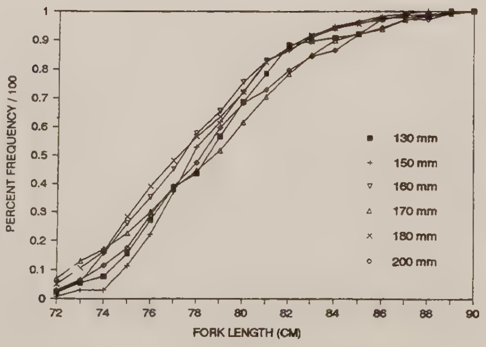


**Figure 3**
Cumulative percent frequency-of-occurrence by fork-length interval for 130 mm, 150 mm, 160 mm, 170 mm, 180 mm, and 200 mm stretch mesh sizes for the 78 cmFL mode of albacore *Thunnus alalunga* sampled in the 1980 JAMARC survey (JAMARC 1983).

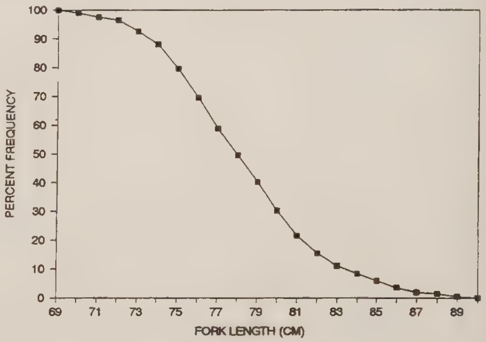


**Figure 4**
Mean selectivity-curve right limb for albacore *Thunnus alalunga* from the 78 cmFL mode sampled in the 1980 JAMARC survey (JAMARC 1983).

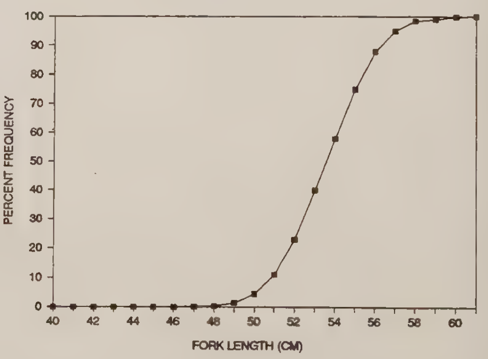


**Figure 5**
Mean selectivity-curve left limb for albacore *Thunnus alalunga* from the 53 cmFL mode sampled in the 1980 JAMARC survey (JAMARC 1983).

These two limbs must now be placed appropriately on the X axis for each mesh size. This is accomplished separately for each limb by mesh size. The sampling efficiency at 53.5 cmFL for each mesh size was estimated by linear regression. The observed maximum percent efficiency of sampling at the 53 cmFL peak was regressed against mesh size for all mesh sizes (Fig. 6). The estimated percent sampling efficiency at 53 cmFL for each mesh size is shown in Table 2. Using the same method, the percent sampling efficiency was estimated for 78 cmFL for each mesh size (Fig. 6, Table 2).

The family of selectivity curves by mesh size is shown in Fig. 7. These were determined by shifting the mean selectivity-curve limbs to the left or right so that sampling efficiencies at 53 and 78 cmFL matched the values in Table 2 for each mesh size. Fork lengths between the two limbs were assumed to be sampled with maximum efficiency, consistent with theory associated with unimodal selectivity curves (Hamley 1975).

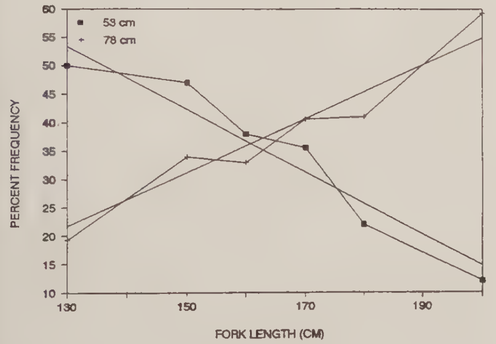


**Figure 6**

Linear regressions of observed maximum percent sampling efficiency at 53 cm and 78 cmFL against stretch-mesh size for albacore Thunnus alalunga.

**Table 2**

Estimated percent sampling efficiency for albacore *Thunnus alalunga* at fork lengths of 53 cm and 78 cm for various stretch mesh sizes.

| Mesh size (mm) | Fork length 53cm | (% efficiency) 78cm |
|---|---|---|
| 130 | 53.3 | 21.7 |
| 150 | 42.3 | 31.2 |
| 160 | 36.8 | 35.9 |
| 170 | 31.3 | 40.7 |
| 180 | 25.7 | 45.4 |
| 184 | 23.5 | 47.3 |
| 200 | 14.7 | 54.8 |

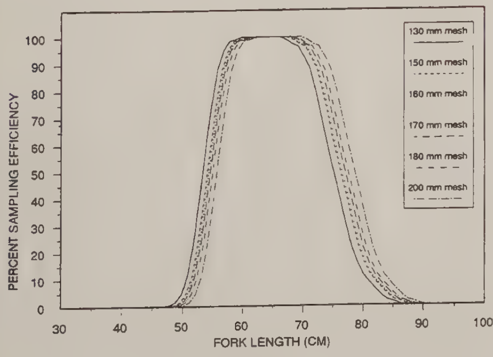


**Figure 7**

Selectivity curves (%) for albacore *Thunnus alalunga* for 130 mm, 150 mm, 160 mm, 170 mm, 180 mm, and 200 mm stretch-mesh sizes.

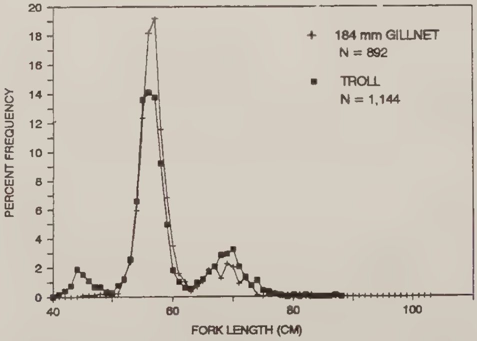


**Figure 8**

Percent frequency-of-occurrence by fork-length interval for albacore *Thunnus alalunga* sampled in the 1985 NMFS experiment by 184mm stretch mesh and by trolling.

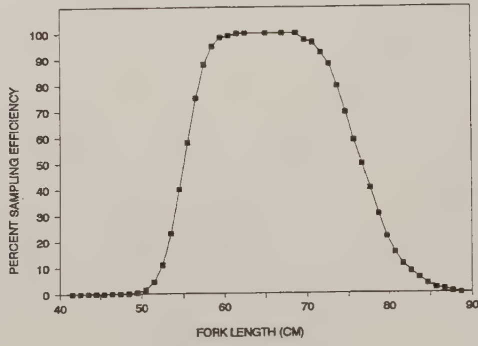


**Figure 9**

Selectivity curve for albacore *Thunnus alalunga* for 184 mm stretch-mesh size.

### NMFS 1985 experiment

Length-frequency data for albacore collected in the 184 mm mesh during the 1985 NMFS experiment are shown in Fig. 8. The estimated selectivity curve is shown in Fig. 9 and, as expected, is almost identical to the 180 mm mesh selectivity curve (Fig. 7). For comparison, length-frequencies from the NMFS experiment taken by both trolling jigs and drift netting in the same area are shown in Fig. 8. As predicted by the selectivity curve (Fig. 9), few fish <50 cm length were sampled by the 184 mm mesh even though the fish were assumed available to the net, as indicated by the size-frequency sampled by the trolling gear fished in the same area and time.

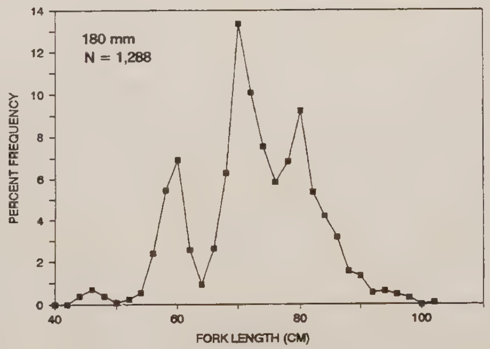


**Figure 10**
Percent frequency-of-occurrence by fork-length interval for albacore *Thunnus alalunga* for 180mm stretch mesh sampled by the 1982 JAMARC survey (JAMARC 1985).

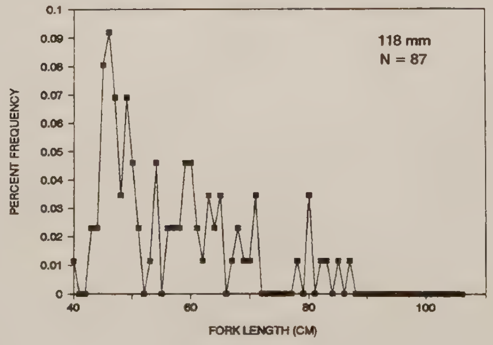


**Figure 11**
Percent frequency-of-occurrence by fork-length interval for albacore *Thunnus alalunga* for 118mm stretch mesh sampled by the 1983 JAMARC survey (JAMARC 1986).

### JAMARC 1982 experiment

The 1982 JAMARC South Pacific experiment collected data for a 180 mm mesh size. Length-frequency data obtained are shown in Fig. 10. The estimated selectivity curve for this mesh is the same as shown for the 180 mm mesh in Fig. 7. From inspection of the length-frequencies for 180 mm and 184 mm mesh sizes from the North Pacific, it was apparent that the South Pacific experiment sampled an albacore population with a different size structure. The results show a much greater proportion of fish in the 70–80 cmFL range than in the North Pacific sampling. This is also seen in samples taken from the U.S. troll fishery that operated in the South Pacific (Rensink 1991)

### JAMARC 1983 experiment

Length-frequency data obtained from the 1983 JAMARC South Pacific experiment using 118 mm mesh are shown in Fig. 11. The selectivity relationships developed from the North Pacific data do not accurately predict the expected selectivity curve for the 118 mm mesh. This is a result of small sample sizes and an observed peak size mode well below the sizes of albacore captured in the mesh sizes used to derive the selectivity curves.

## Discussion

Selectivity curves derived from the JAMARC 1980 experimental data appear similar in shape to selectivity curves presented for salmon *Onchorynchus nerka* and *O. keta*, slender tuna *Allothunnus fallai*, and mackerel *Scomberomorus niphonius*, and other fusiform fishes (Taguchi 1961, Ishida 1964, Shimazaki et al. 1984). The asymmetry of each selectivity curve (i.e., steeper on the left limb and flatter on the right limb) is similar to that observed for selectivity curves of other fusiform fishes (Hamley 1975) and is explained by the mechanics of capture. The smallest fish, retained by the net at some particular girth/mesh-perimeter ratio, tend to be caught near maximum girth. Also, the range of sizes providing the ratio is relatively narrow. For larger fish, the same ratio can be found over a larger range of fish sizes because the point of capture may be anywhere from the maximum girth forward to the snout tip. For example, maximum girth of albacore increases more rapidly than opercular girth as a function of length (Fig. 12) which extends or skews the

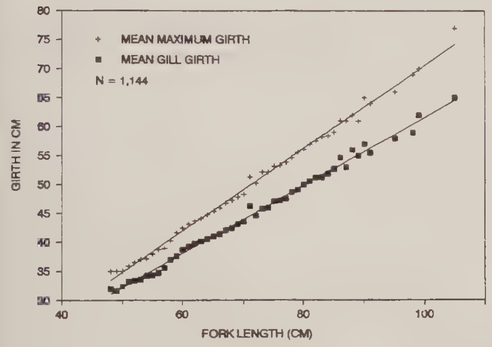


**Figure 12**
Relationship of albacore *Thunnus alalunga* maximum and opercular girths to fork length for 1144 fish sampled by the 1985 NMFS experiment.

right limb of the selectivity curve. This skewing can be troublesome when symmetrical or pre-determined selectivity curves are fit to data. The method used in this study minimizes this problem.

Assumptions that selectivity curves estimated from the 1980 JAMARC experiment applied to similar nets, such as the NMFS 184 mm mesh and the JAMARC-1982 180 mm mesh, appear acceptable from the data available. The principal factor limiting the application of these selectivity curves to other albacore populations is the girth/length relationships discussed above (Fig. 12). Significant changes in this relationship will change the steepness of the selectivity-curve limbs and the skewness.

Extrapolation of the mean selectivity curve to smaller mesh sizes than those providing the initial data may be improper based on the data observed for the 118 mm mesh. Although the sample size was relatively small, the apparent increase in tangling of larger fish caught in smaller mesh sizes compared with larger mesh sizes suggests that the right portion of selectivity curves for meshes <130 mm are more skewed. Tangled fish did not appear to be a problem in the NMFS or JAMARC 1980 datasets, presumably because all mesh sizes either gilled or wedged fish in the largest mode. Additionally, there may have been fewer larger fish available in the survey areas, as shown by troll-caught samples.

The absence of larger, tangled fish in both net-caught and troll-caught samples could result from reduced availability or vulnerability of larger fish in the areas sampled. Surface fisheries (i.e., drift net, troll, and pole-and-line) for albacore in the North Pacific produce catches with similar length-frequencies in the same areas (Bartoo & Foreman In press). However, albacore taken by subsurface longline gear at the same time and area are generally larger in length than those taken in the surface fisheries. This indicates albacore show differential availability or vulnerability between surface and subsurface gears. This could be due to spatial separation or behavior which may change with fish size. The results presented here assume that vulnerability to DGNs is relatively static over time.

## Acknowledgments

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9311

# Evidence of Interactions Between High Seas Driftnet Fisheries and the North American Troll Fishery for Albacore

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## I. ABSTRACT

During the 1990 North American albacore troll fishery, observers aboard United States troll vessels examined 19,526 albacore for evidence of driftnet damage. Results indicate that 13.4% of the albacore caught encountered driftnets. Proportions varied by area fished.

## II. INTRODUCTION

The Southwest Fisheries Science Center (SWFSC) in cooperation with members of the Western Fishboat Owners Association (WFOA) placed fisheries observers on U.S. trollers fishing in the North Pacific in 1990. This was part of a comprehensive impact assessment program on the effects of the high seas driftnet fisheries on the North Pacific albacore (*Thunnus alalunga*) stocks and other fisheries. Albacore which escape driftnets bear some external marks that provide direct evidence of interaction. Throughout this report, we refer to these external marks from driftnet encounters as damage. Damage may be minor or severe, and may include marks on the skin, bruising, and cuts and broken skin (loss of scales), missing areas of skin, and scars from any of the foregoing. This report describes the results of the 1990 observer project.

### 1. Background

Catches and catch-per-effort from the U.S. albacore troll and pole-and-line fisheries in the North Pacific have declined since the mid-1970's (Coan *et al.* 1991; Kleiber and Perrin In Press). In addition to the U.S. fishery, Japan and Taiwan each have a surface fleet and a longline fleet catching albacore in the North Pacific. Three high seas driftnet fleets also catch albacore in the North Pacific (Anon. 1989).

The small mesh (90 - 120 mm stretched mesh) driftnet fleets are made up of vessels from Japan, Taiwan and the Republic of Korea (ROK). The Japanese and Taiwanese fleets fish for flying squid (*Ommastrephes bartrami*) in the North Pacific Transition Zone from about May through December. The ROK fleet operates there the entire year. The incidental catches of albacore by these driftnet fisheries are not precisely known.

The large mesh (160 - 180 mm stretched mesh, Bartoo and Holts 1991) driftnet fleet is made up of vessels from Japan and Taiwan. Albacore is a major component of that catch. Taiwan has a developing large mesh fishery for albacore. The impact of these fleets on albacore is largely unknown. Taiwan and Japan have imposed internal regulations on their driftnet fleets to limit fishing effort in the higher latitudes and minimize interceptions of high seas salmon.

Although driftnet catches and landings for North Pacific albacore are incomplete and unreported for some fleets, the aggregate reported annual landings for driftnet fisheries exceeded 20,000 mt in 1988 (Tsuji *et al.* 1992). In the mid-1980's U.S. albacore fishermen began reporting increasing numbers of albacore injured or scarred by encounters with high seas driftnets. Concerns focused on the impact of driftnet fisheries on the North Pacific albacore stock and the direct interaction with the U.S. albacore troll fleet.

## 2. Troll Observer Project

In 1990, SWFSC biotechnicians observed 6 complete fishing trips aboard 5 different troll vessels. Vessels were selected to provide data over the entire season and cover the entire fishing area. The cruise tracks of the observed vessels are shown with the entire catch distribution of the troll fleet in Figure 1. The fishery followed eastward migrating albacore beginning north of Hawaii in June, moved eastward to 135°W in July, and remained east of 135°W in August and September (Coan *et al.* 1991). Operations and observations covered a wide area of the North Pacific Ocean. The project goals were to document and estimate the interaction between high seas driftnet and North American troll fisheries, and to provide biological information from which delayed mortality of albacore due to net encounters might be inferred. Specific objectives are as follows:

A. Describe the type and severity of driftnet damage on troll-caught albacore.
B. Estimate the relative frequency of undamaged albacore and damaged albacore.
C. Estimate the size-frequency of undamaged albacore and damaged albacore.
D. Determine the relative physiological condition of troll-caught albacore that show gillnet damage.

Here, we report results relating to the first 3 objectives.

## III. METHODS

Driftnet marks are most visible when the fish is boated. Most marks disappear or are rendered indistinguishible once the fish is frozen or dies on deck. Observers examined each fish landed and noted net scars or marks using a set of reference photographs detailing the type and severity of injuries (Figure 2). These were coded as:

| Code | Damage Description |
|---|---|
| 0 | No gill net damage to fish. |
| 1 | Minor damage along side(s) of fish, pattern of stripes due to minor scale loss where fish forces its way through or along the net. |
| 2 | Minor damage to head, chiefly forwards of pectoral fins, brush-like pattern of scale loss. |
| 3 | Severe damage with bruising or scraping away of parts of the skin, primarily in area of greatest girth and mostly on dorsal surface. |
| 4 | Old gill net damage of any degree that is partially or completely healed. These are assumed to have occurred previously. |

Observers photographed, for later analysis, fish which showed damage but could not be classified on board.

In addition to damage code, observers collected information on fork lengths, maximum girth, and weights for as many fish as possible. Fishing operations usually continued all day from first light to just after dark.

## IV. RESULTS

Six cruises, totalling 377 observed sea-days were completed between the end of May and the end of October 1990. A total of 25,177 albacore were caught and boated during the cruises. Seventy-eight percent of these (19,526) were examined for driftnet related injuries and measured for fork length and maximum girth. A total of 8,720 fish were weighed to the nearest pound (transformed to kg). Catch-per-fishing-day averaged 66.8 fish-per-day but varied considerably between cruises (Table 1). One vessel (Cruise 5) was on a charter with WFOA as a scout boat and did not fish routinely.

Albacore of three distinct size modes were caught throughout the North Pacific apparently representing 2, 3, and 4 year old fish (Bartoo and Foreman In Press; Fig. 3). Length modes were at 54, 65 and 80 cm corresponding to weights of 3.5, 5.7, and 10.6 kg.

Overall, 86.6% of the observed catch showed no evidence of net related damage (Table 2). Recently damaged albacore (damage codes 1,2 & 3) totalled 9.2%, while an additional 4.2% had healed scars, possibly from net encounters during the previous fishing season (code 4). Within the recently damaged albacore, 3.5% had minor damage; 5.2% had moderate injuries on the head, gill covers and fins; while 0.5% had severe bruising with significant loss of scales with skin damage to their head, sides and fins.

Observers measured fork lengths (FL) of 11,868 albacore east of 140°W in July, August and September and 7,658 albacore west of 140°W in June and July. The catch taken west of 140°W had larger fish than the catch east of 140°W (Fig. 4). These large fish averaged 9 - 11 kg (20 to 25 lbs). Although the sample size was small, injuries from recent encounters with driftnets were observed on nearly 18% of the catch.

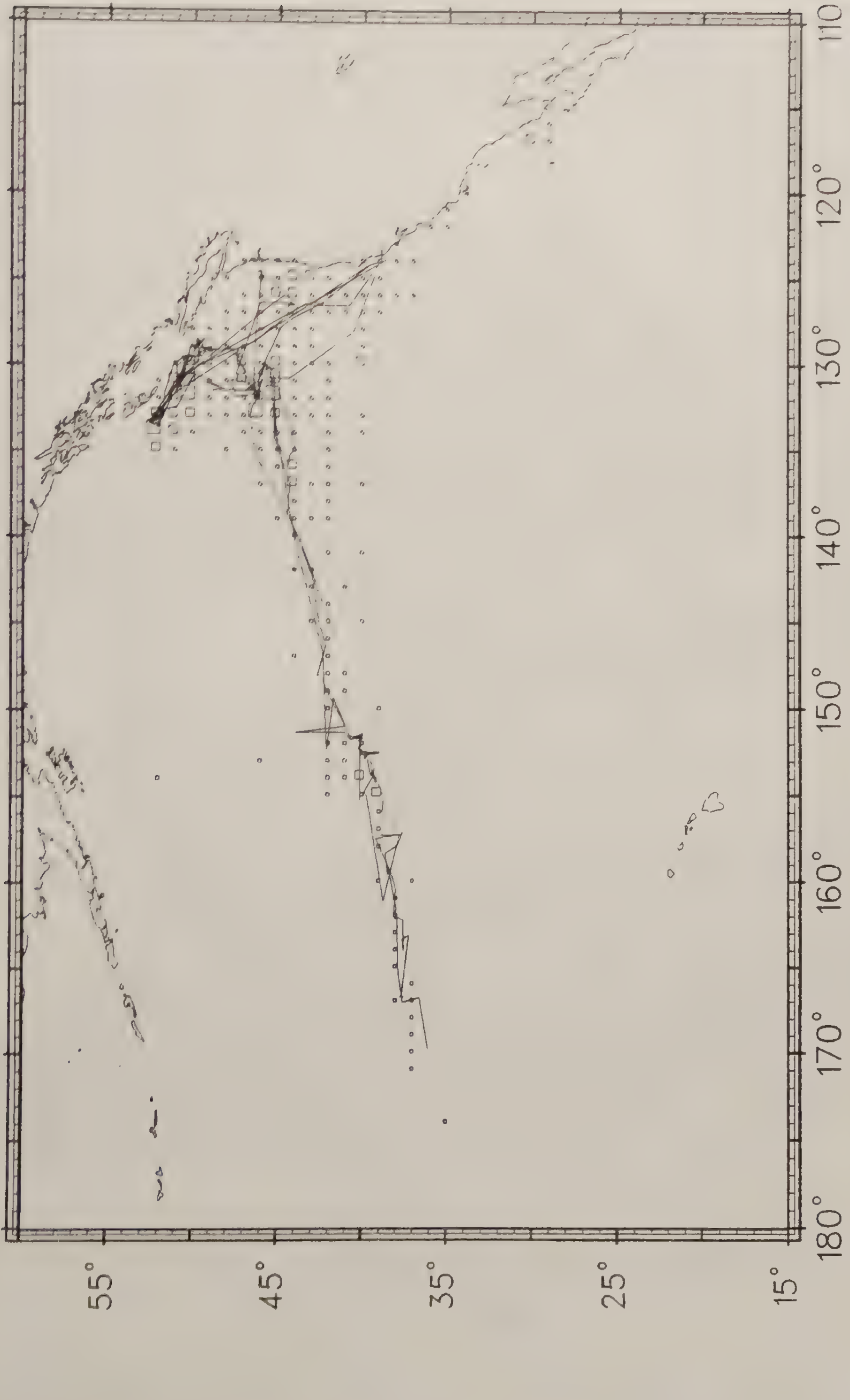

Figure 1. Cruise tracks for the observed albacore troll vessels and the distribution of the 1990 U.S. troll catch (squares). (small squares are catches of 1-1000 fish, medium = 1001-10000 fish, large = +10000 fish). Three vessels departed Honolulu and three departed from the mainland. All cruises terminated on the west coast of United States.

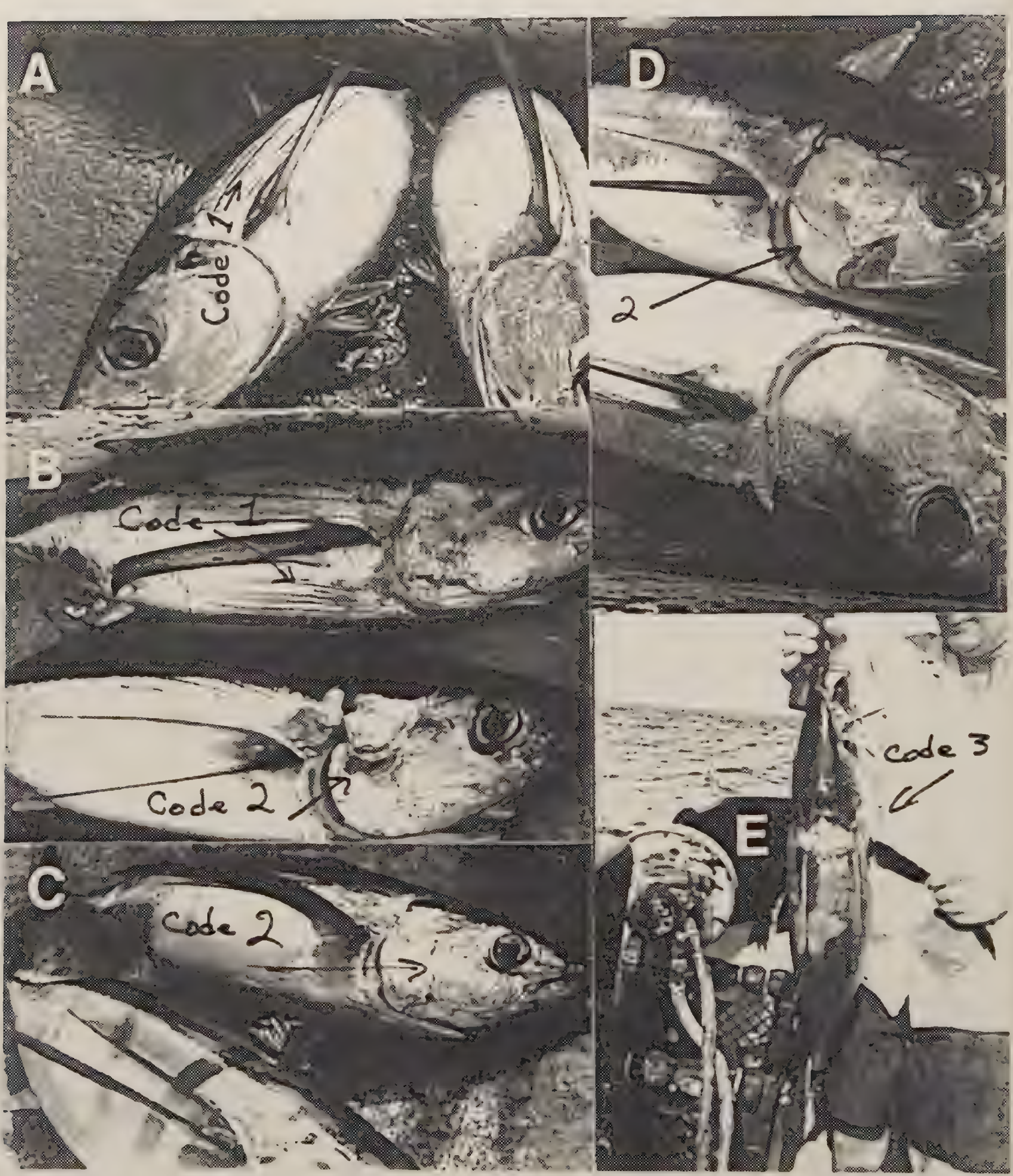
A
Code 1
B
Code 1
Code 2
C
Code 2
D
2
E
Code 3

Figure 2. Pacific albacore damaged by high seas driftnets. Damage code 1 indicates minor scratches and scale loss (A & B). Damage code 2 shows moderate damage on the head (B, C & D). Damage code 3 indicates significant loss of scales or skin (E).

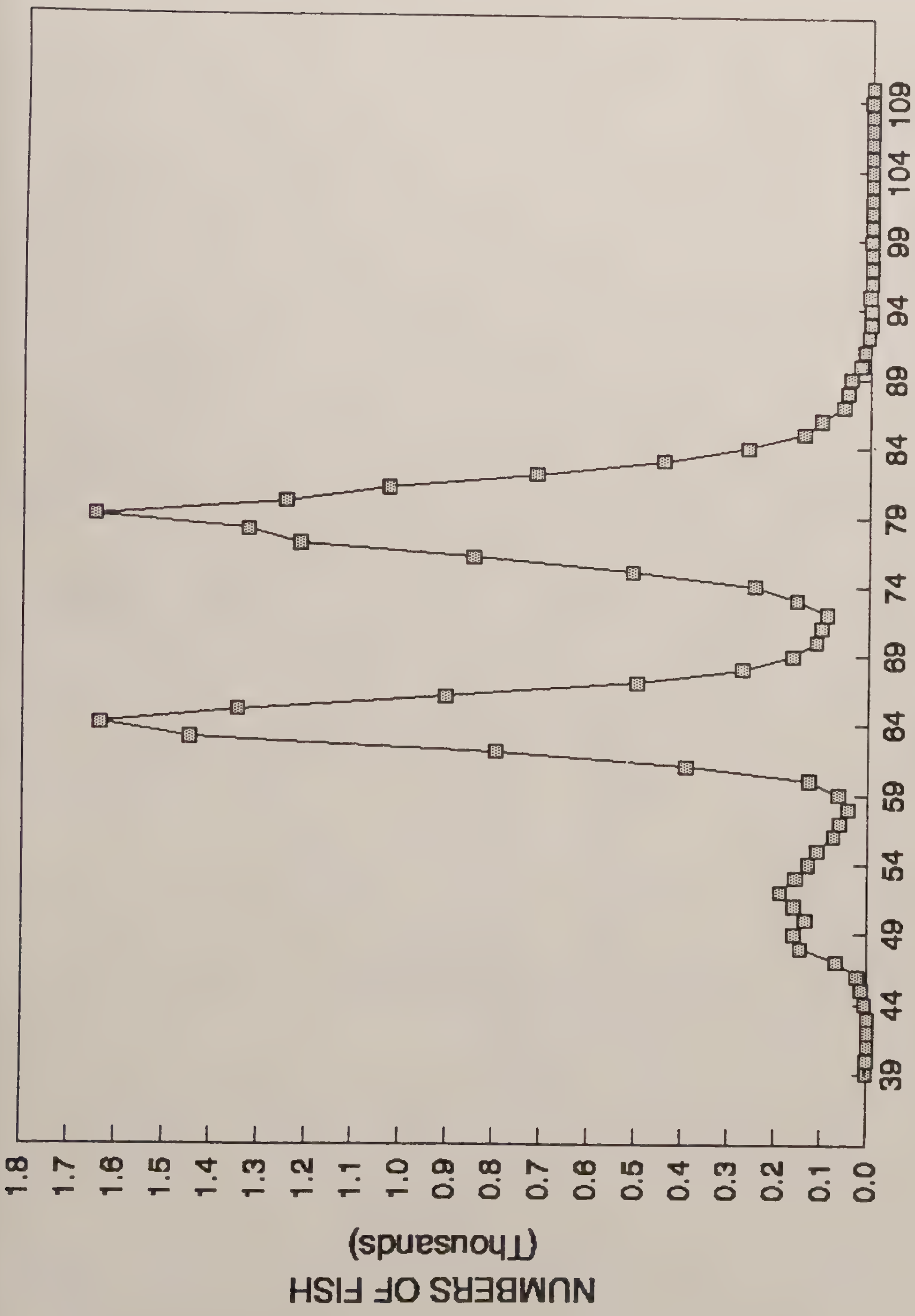

Figure 3. Length frequency of 19,526 albacore measured during the 1990 troll fleet observer program.

Table 1. Albacore CPUE (fish/day) by cruise.

| Cruise | Mean | Range | SD | 95% C.I. |
|---|---|---|---|---|
| Cruise 1 | 108 | 0 - 634 | 146.3 | 76.01 - 139.9 |
| Cruise 2 | 68 | 0 - 363 | 91.3 | 48.47 - 88.1 |
| Cruise 3 | 88 | 0 - 291 | 58.5 | 74.02 - 101.3 |
| Cruise 4 | 48 | 1 - 122 | 30.1 | 39.20 - 56.5 |
| Cruise 5 | 10 | 0 - 100 | 22.8 | 2.63 - 18.3 |
| Cruise 6 | 58 | 0 - 375 | 82.7 | 20.02 - 95.3 |

Table 2. Percent of albacore by fishing area damaged during encounters with driftnets and caught by troll vessels.

| | FISHING AREA | | | | |
|---|---|---|---|---|---|
| DAMAGE TYPE | WEST OF 160°W | 160°W TO 140°W | NORTH OF 50°N | EAST OF 140°W AND SOUTH OF 50°N | μ ALL AREAS |
| NO DAMAGE | 81.2 | 82.8 | 94.1 | 88.4 | 86.6 |
| NEW DAMAGE | | | | | |
| CODE 1 | 6.0 | 4.9 | 0.0 | 3.0 | 3.5 |
| CODE 2 | 11.4 | 6.3 | 0.4 | 2.7 | 5.2 |
| CODE 3 | 0.5 | 0.5 | 0.0 | 1.0 | 0.5 |
| TOTAL NEW DAMAGE | 17.9 | 11.7 | 0.4 | 6.7 | 9.2 |
| OLD DAMAGE | 0.9 | 5.5 | 5.5 | 4.9 | 4.2 |
| SAMPLE SIZE, n | 218 | 7,440 | 4,800 | 7,068 | 19,526 |

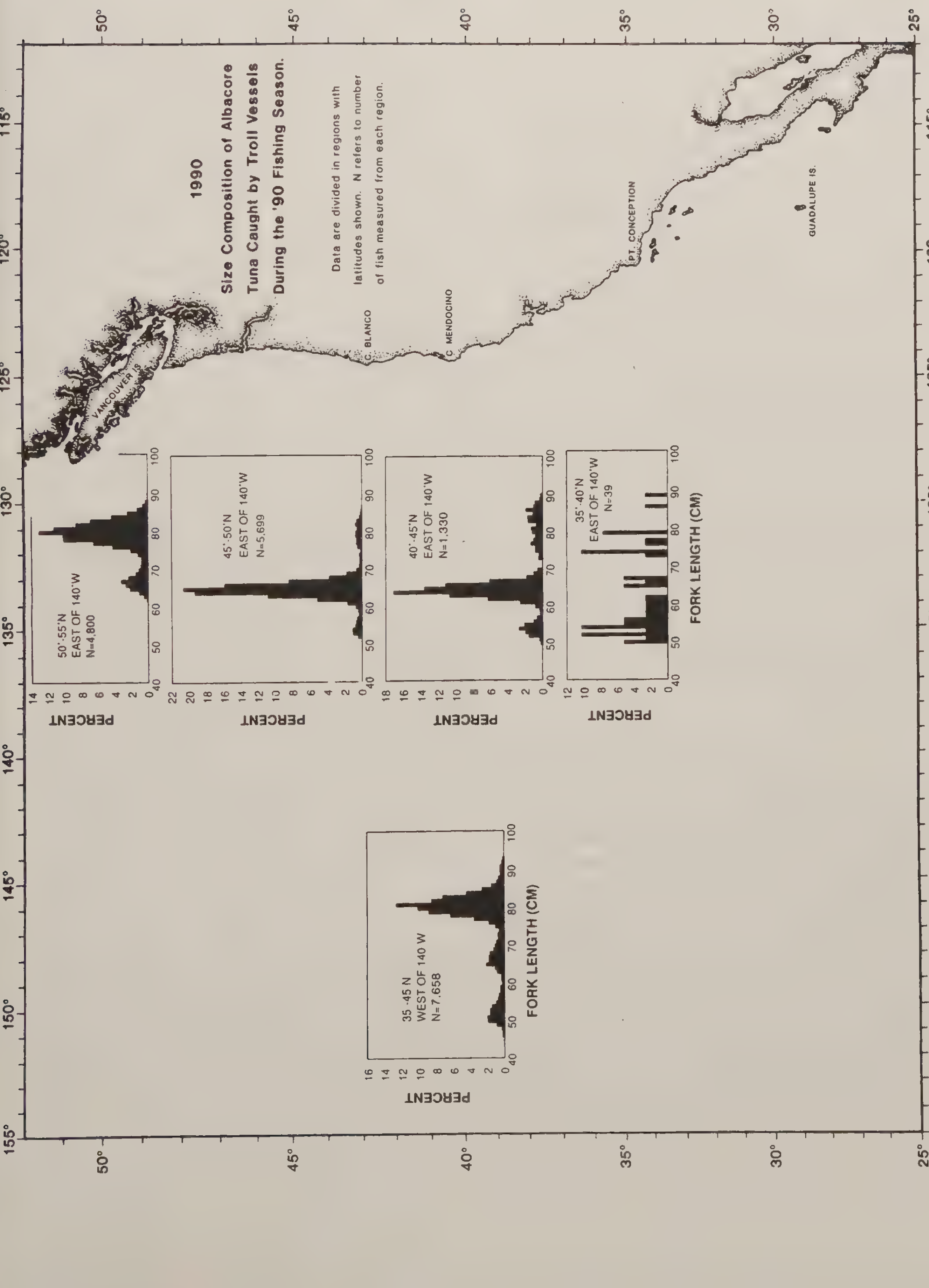

Figure 4. Albacore length frequencies by fishing areas of the North Pacific.

Old and healed scars, from a previous time, appeared on less than one percent of the catch west of 160°W but increased to about 5% east of 160°W (Table 2).

By the end of July, all observed vessels were fishing east of 140°W and south of 50°N, catching fish weighing 5 - 9 kg (12 to 20 lbs). These fish were caught throughout the month of August and early September. The incidence of fresh injuries remained at about 6.7% in the coastal areas and the incidence of old injuries remained fairly constant at about 5 percent.

Albacore taken north of 50°N had a higher proportion of large (80 cm FL) fish than those caught east of 140°W and south of 50°N (Figure 4). No fish less than 63 cm FL were sampled north of 50°N. Fishing remained moderately good north of 50°N until seasonal storms out of the Gulf of Alaska forced many fishing vessels to return home by the end of September. Few recently damaged fish were observed north of 50°N although the proportion of old and healed damage changed little from that seen just off Washington and Oregon (5.5% to 4.9% respectively).

The observed length frequencies varied considerably in different fishing locations. Length frequencies of injured fish did not vary greatly from uninjured fish within each area examined. The length frequencies, by area, for undamaged (code 0), recently damaged (codes 1-3) and old damage (code 4) are shown in Figures 5, 6 and 7 respectively. No previous damage estimates are available from the 1989 season that could help describe survival of fish sampled (code 4) in the 1990 fishing season.

The length-weight relationship for all 8,720 weighed albacore is shown in Figure 8.

## V. DISCUSSION

Our results show that 13.4% of the albacore caught encountered driftnets. These proportions are less than some reports from fishermen which ranged from 40% to 90% of the catch. Our data do indicate considerable variation in damage on a daily basis, ranging from none to 100% of the catch. Our results are consistent with those reported for albacore in the south Pacific which ranged from 4.5% to 14.5% of the catch in 1989 and 1990 (Hampton *et al.* 1991).

Our results show that 9.2% of the 1990 catch evidenced new damage and that higher proportions were found to the west. The apparent "gradient" in proportion of net marked fish from west to east may be explained by the migration pattern of albacore and the timing and location of the driftnet and troll fisheries. Additionally increased short-term mortality of a few days or weeks due to net damage may contribute.

Based on tag information the migration pattern of juvenile North Pacific albacore of the size caught by the driftnet and troll fisheries is predominately east-west (Otsu and Uchida 1963, Clemens 1961). The fish move from waters off Japan in the spring across the Pacific in the Subarctic Transition Zone (STZ) and enter the coastal waters of North America in July. In late September albacore leave the east Pacific and return to waters off Japan. This annual pattern may be repeated until age 5 or 6. Although some portion of the population makes the complete trip across the Pacific in just a few months it is apparent that a considerable proportion of the population is not available at the extreme ends of the population distribution (Bartoo and Foreman in press).

The troll fishery as shown in Figure 1 begins near the mid-Pacific in May or June and moves with the advancing albacore to the east. Both small and large mesh driftnet fisheries in 1990 were distributed as shown in Figure 9 with most of the effort centered between 170°E and 170°W and becoming less east of 170°W. Collectively these fisheries operate the year around with considerably higher effort east of 170°E after May.

Higher proportions of marked fish are seen west of 140°W where the driftnet and troll fisheries overlap in area and time. Lower proportions of marks are seen east of 140°W, outside the distribution of the driftnet fisheries. Additionally, some albacore may migrate into the troll fishery from areas south of the driftnet fishery distribution (Laurs and Lynn 1977) and dilute the marked portion of the population.

The proportions of marked fish in the east may also be decreased by an increase in mortality associated with encountering and escaping a driftnet (alive) which reduces the number of albacore available to be recaptured in the troll fishery. This would logically seem to increase directly with the severity of injury and passage of time (as the albacore move eastward).

## VI. ACKNOWLEDGEMENTS

We wish to thank the Western Fishboat Owners Association for their help in locating owners of fishing vessels for placement of our observers. We also want to thank the owners of those vessels for their support. We are truly indebted to the observers who examined and measured the nearly 20,000 albacore. Finally, thanks to the reviewers whose suggestions greatly improved this manuscript.

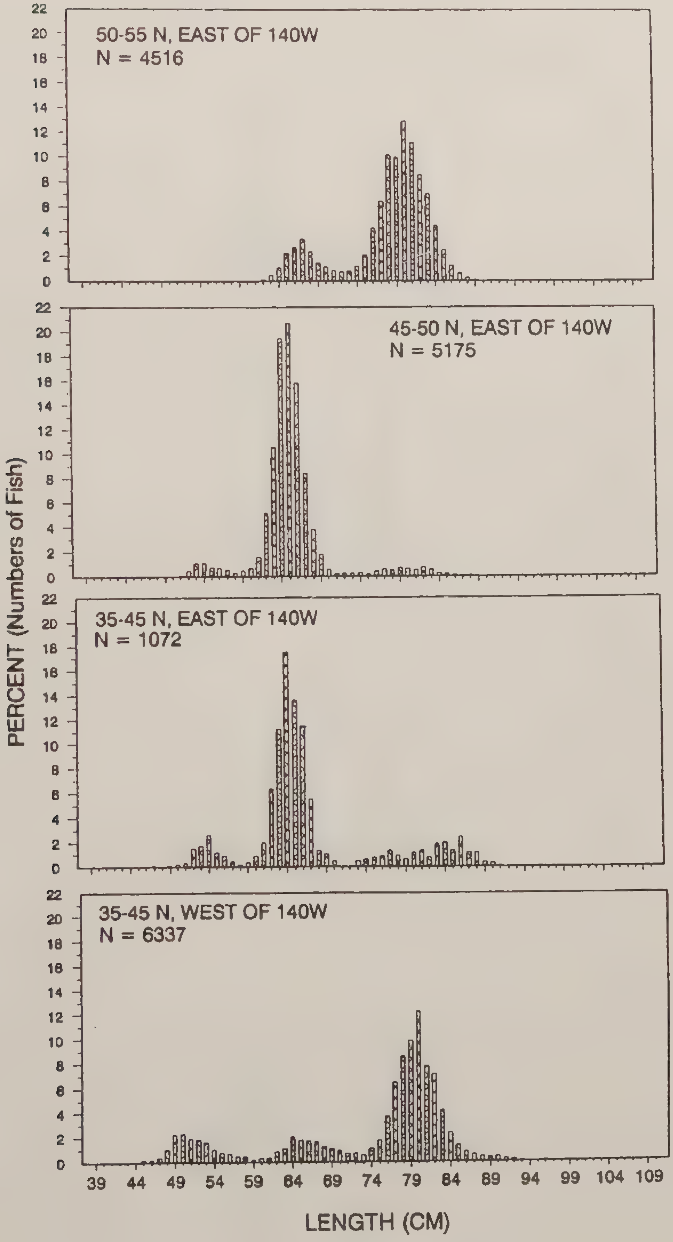

Figure 5. Length frequencies of undamaged albacore (Code 0) from the four fishing areas of the North Pacific.

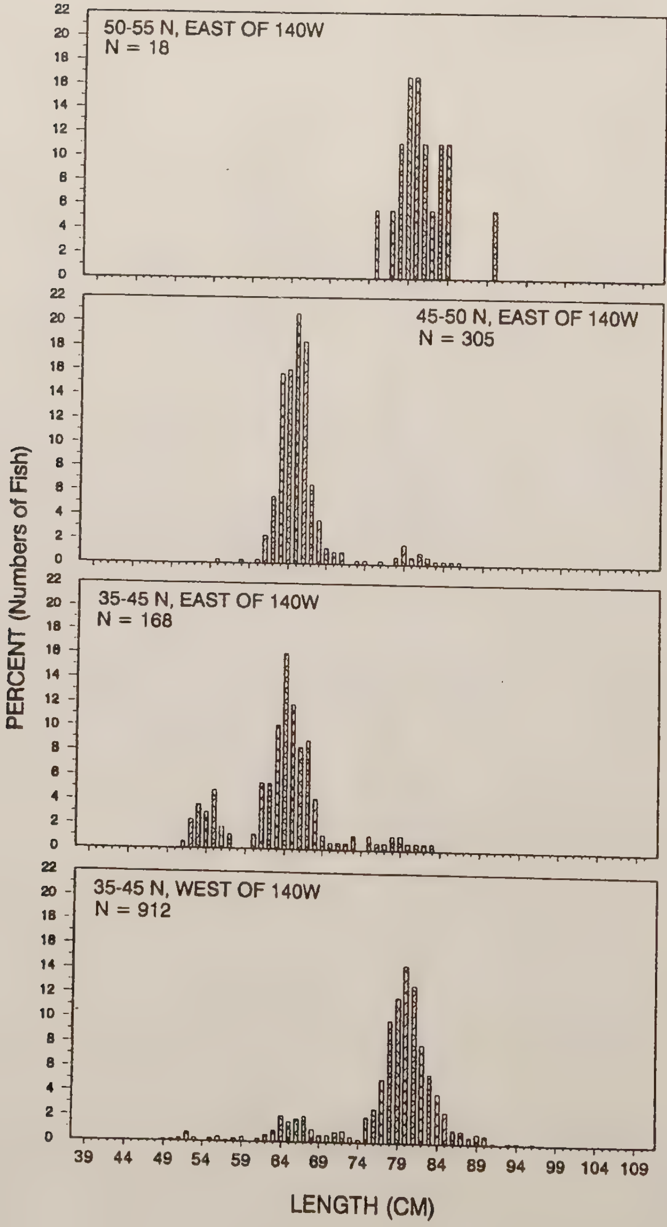

Figure 6. Length frequencies of recently damaged albacore (Codes 1, 2, and 3).

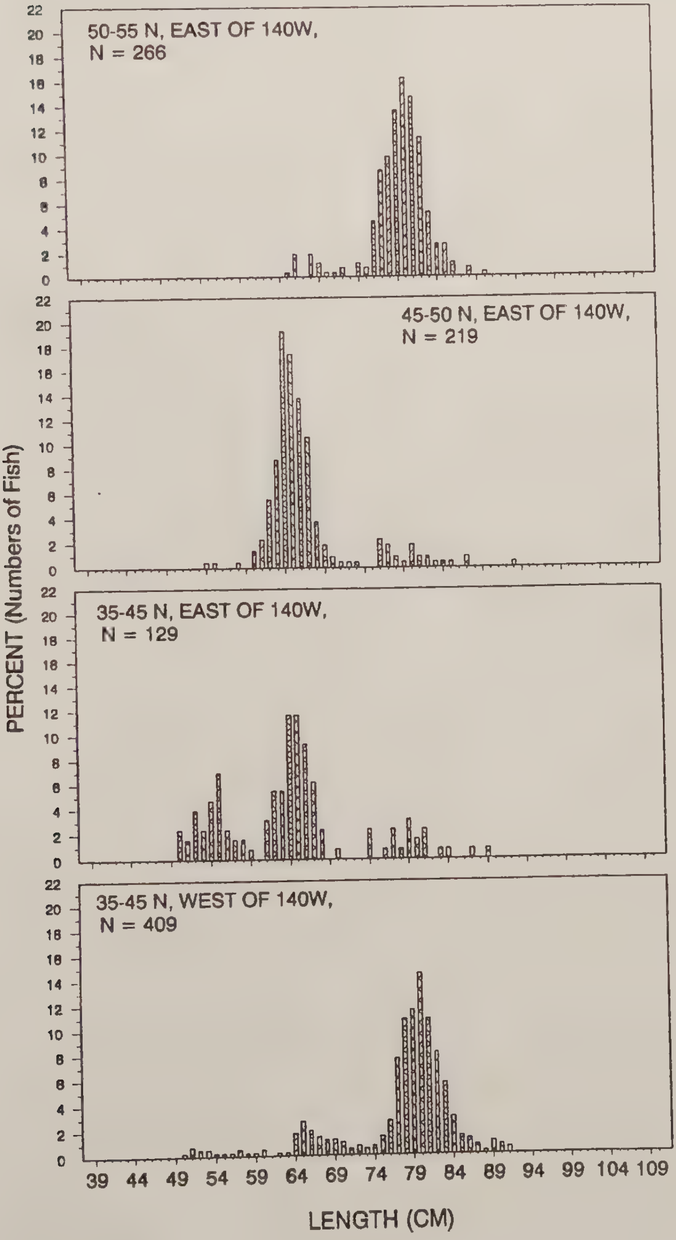

Figure 7. Length frequencies of albacore with old injuries (Code 4).

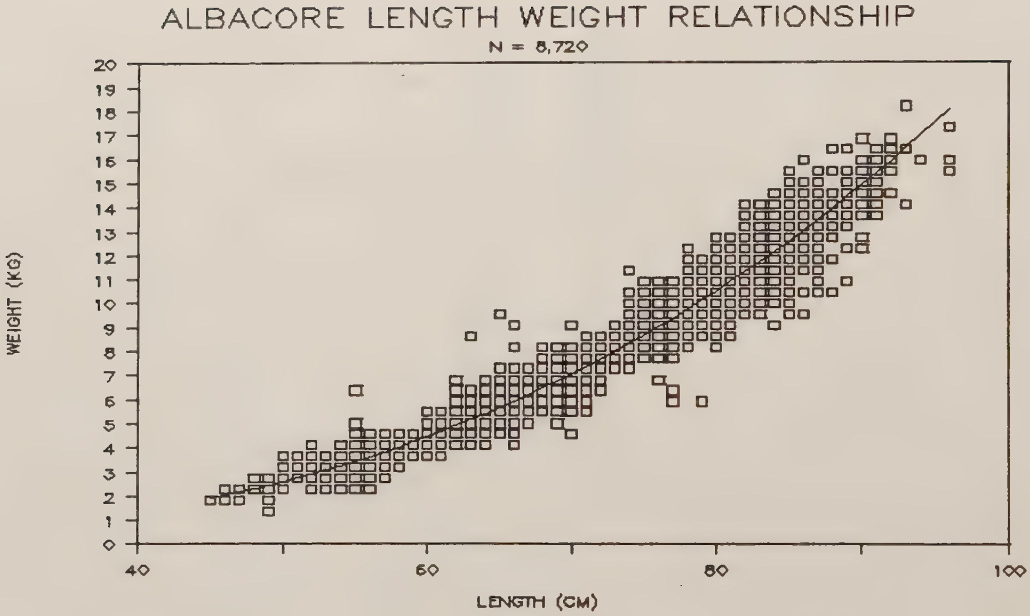

Figure 8. Length-weight relationship of albacore weighed during the troll fleet observer program.

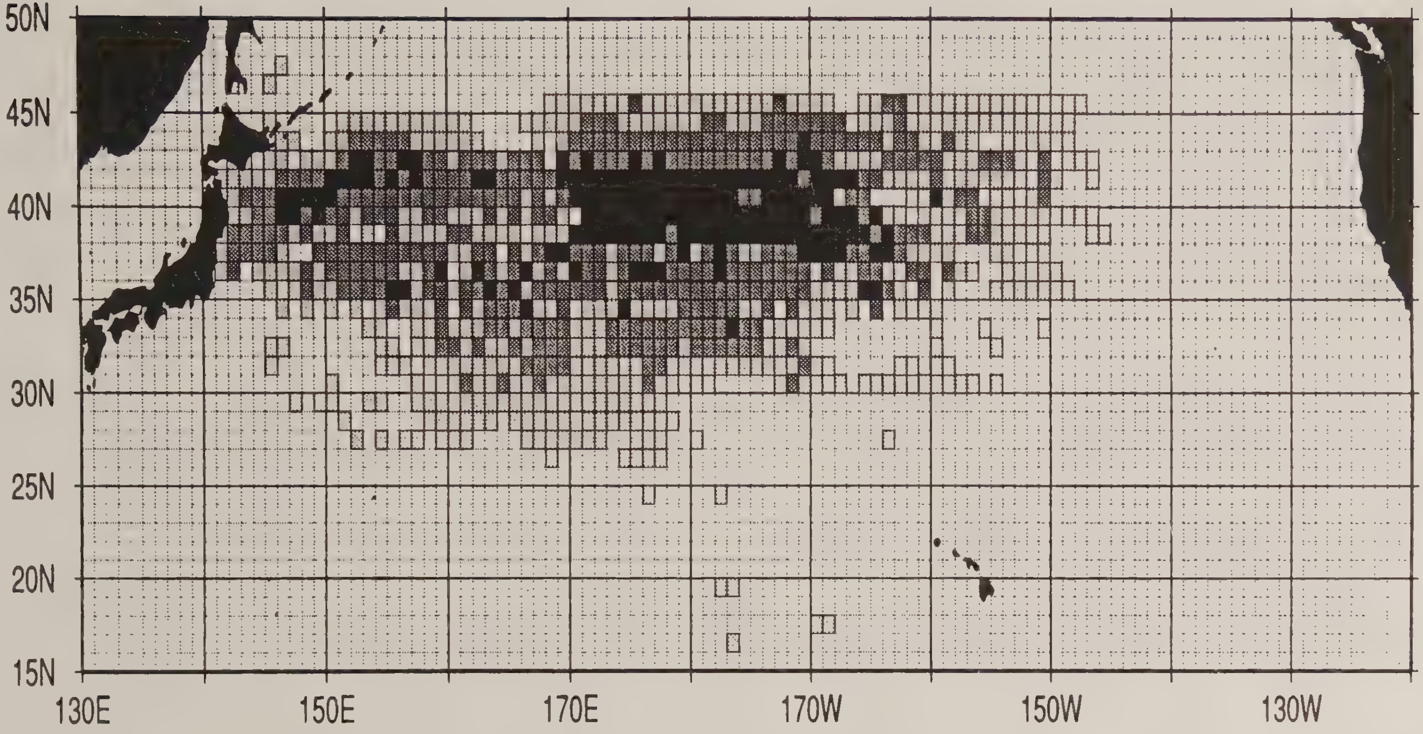
50N
45N
40N
35N
30N
25N
20N
15N
130E
150E
170E
170W
150W
130W

Figure 9. Distribution of observed driftnet effort in the North Pacific Ocean in 1990 for both large and small mesh fisheries. Intensity of effort is shown by shading. (Personal Communication, J. Wetherall, Nat. Mar. Fish. Serv., Honolulu, HI.)

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# Influence of Age-Selective Surveys on the Reliability of Stock Synthesis Assessments

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We used Monte Carlo simulations to examine the reliability of assessments following a method of separable catch-at-age analysis (Methot's stock synthesis approach). Our simulations were based on the widow rockfish (*Sebastes entomelas*) fishery off the west coast of the continental United States. We designed the study to examine how the performance of the method depended upon the age-specific selectivity pattern of a survey of relative abundance. When survey selectivity increased asymptotically with age, stock synthesis estimates of final year biomass (and most other parameters) tended to be closest to the correct value. When the survey concentrated on young fish the estimates were least reliable. When the survey selectivity was "dome-shaped," concentrating on intermediate-aged fish, estimates were somewhat less precise (and less accurate) than for the asymptotic pattern but much more precise than for the survey concentrating on young fish. Predictably, estimates of recruitment and biomass were better at a higher fishing mortality rate and when the magnitude of survey error was lower. Generally, mean errors in estimated biomass and recruitment were positive, while median errors were close to zero. This pattern is due to transformation bias associated with a lognormal error structure.

Nous avons utilisé des simulations de Monte-Carlo afin de déterminer la fiabilité d'évaluations réalisées par analyse à composantes séparables des prises selon l'âge (synthèse des stocks de Methot). Nos simulations étaient fondées sur la pêche de la veuve (*Sebastes entomelas*) réalisée au large de la côte ouest des États-Unis. Nous avons conçu l'étude de façon à déterminer dans quelle mesure le rendement de la méthode dépendait de l'allure de la sélectivité spécifique quant à l'âge d'un relevé de l'abondance relative. Lorsque la sélectivité du relevé augmentait de façon asymptotique avec l'âge, l'estimation par synthèse du stock de la biomasse de dernière année (et de la plupart des autres paramètres) tendait à se rapprocher le plus de la valeur réelle. L'estimation la moins fiable était obtenue lorsque le relevé portait surtout sur les poissons les plus jeunes. Lorsque la sélectivité du relevé correspondait à la forme "en dôme" et portait donc sur les poissons d'âges intermédiaires, l'estimation était quelque peu moins précise (et moins exacte) que celle du relevé d'allure asymptotique, mais demeurait plus précise que celle du relevé portant surtout sur les jeunes poissons. Comme on peut s'y attendre, l'estimation du recrutement et de la biomasse était meilleure lorsque le taux de mortalité par pêche était plus élevé et que l'erreur du relevé était plus faible. De façon générale, l'erreur moyenne de la biomasse et du recrutement estimé était positive tandis que l'erreur médiane se rapprochait de zéro. Ce phénomène s'explique par des erreurs de transformation liées à un biais de structure lognormale.

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Separable age-structured population models are widely used to analyze fishery catch-at-age data in order to estimate recruitment, fishing mortality rates, and stock abundance. These models assume that the fishing mortality rate can be separated into a product of year and age effects (Doubleday 1976). In most instances, a wide range of solutions to a separable model can fit a set of fishery age-composition data about equally well (Doubleday 1976; Deriso et al. 1985; Shepherd and Nicholson 1986). Thus, for reasonably accurate estimates of abundance, separable models require auxiliary data such as information about abundance from trawl surveys or measures of fishing effort (Doubleday 1976; Deriso et al. 1985; Kimura 1990; Methot 1990).

In this paper, we examine the performance of a separable model when survey data on the relative abundance of a stock are available. Our objective is to compare the merits of surveys with different types of age-specific selectivity patterns. Surveys that cover the habitat occupied by adult fish sometimes have selectivity increasing to an asymptote (Rollefsen 1953). Other surveys that use selective gear (e.g., gill net or hook-and-line) or concentrate in a subhabitat occupied predominantly by certain ages may have either a dome-shaped selectivity with peak selectivity at an intermediate age (e.g., Hamley 1975; Methot and Hightower 1990; Ralston 1990) or peak selectivity on recruits (young fish) (Methot and Hightower 1990; Wyllie Echeverria et al. 1990). The separable model we use belongs to Methot's (1990) family of stock synthesis models, which are widely used in assessing fish stocks off the west coast of North America (PFMC 1990). We fit the model to simulated data based on the biology of widow rockfish (*Sebastes entomelas*), which supports a significant trawl fishery off the west coast of the continental United States. This species, like other *Sebastes*, is relatively long-lived, with a maximum reported age of 50 yr in California and an estimated natural mortality rate of 0.15. Although we used the biology of widow rockfish as a basis for our modeling, our goal was to determine general results regarding the performance of the stock synthesis model, not to mimic the widow rockfish fishery exactly.

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## Simulation Design and Methodology

The basic stock synthesis approach is to invoke a dynamic model both of the fishery and of the process by which data are generated and then fit this model to the available data (Methot 1990). The synthesis model estimates a suite of parameters and uses these along with prespecified constants to calculate fitted data values. These fitted or "synthetic data" are then compared with the observed data in likelihood equations, and a search is done for the set of parameter estimates that maximizes the likelihood.

We examined the performance of the stock synthesis model by Monte Carlo simulation. We did 200 simulations for each of the 18 combinations of age-specific selectivity patterns for the survey, average fishing mortality rates during the simulations, and levels of survey error.

We considered surveys with (1) increasing asymptotic selectivity, (2) dome-shaped selectivity, and (3) maximum selectivity for young fish (recruits) (Fig. 1). For each survey selectivity pattern, we used two average levels of fishing mortality (low: mean fishing mortality rate at age 10 ($F$) = 0.075 (half the natural mortality rate, i.e., $M/2$ and high $F$ = 0.30 ($2M$)) and three levels of survey error: low (CV = 10%), medium (CV = 25%), and high (CV = 50%). Note that all cases started in an unfished condition, which is a reasonable portrayal of the widow rockfish fishery prior to 1980. The range of error in surveys is in accord with typical estimates of survey precision (e.g., Rivard 1981; Pope 1983; Pope and Gray 1983; Weinberg et al. 1984).

We first describe the synthesis model used in our simulations, then describe how we generated simulated data sets, and lastly turn to details on how the "best fit" of the synthesis model to the simulated data sets was achieved for each run. With only minor exceptions discussed below, the model fitted in the simulated assessments (i.e., the synthesis model) was the same as the model we used to produce the simulated data sets. That is, our evaluation of the stock assessment methodology did not include appreciable process error.

### Stock Synthesis Model

Following after Lenarz and Hightower's (1988) assessment of the widow rockfish fishery, nine age groups of fish were included in the synthesis model (age 5 through 13+), and we followed the population for a 15-yr time period. The numbers of fish of each age group, starting with age 6, present at the beginning of the first year ($N_{a,1}$, $a$ = 6, ..., 13) and the number of age 5 fish recruiting at the beginning of each year ($N_{5,y}$, $y$ = 1, ..., 15) were estimated as formal parameters as described below. Given estimates of initial numbers and recruitment, the numbers of age $a$ fish at the beginning of each year $y$ after the first ($N_{a,y}$, $a$ = 6, ..., 12; $y$ = 2, ..., 15) were simply the survivors from the previous year:

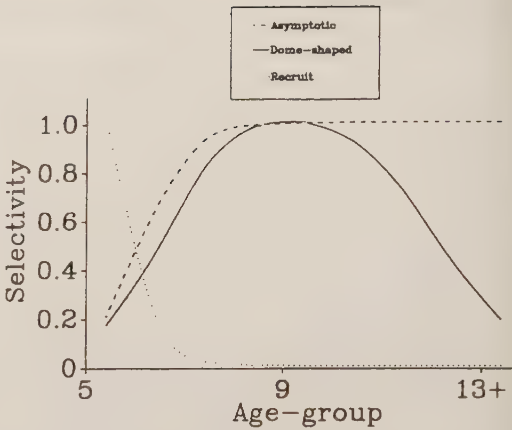

FIG. 1. Selectivity functions for the survey. Note that the dome-shaped function was also the fishery selectivity pattern. Parameters used to generate these functions are given in Table 1. Selectivity has been renormalized, for this presentation only, so that the maximum value is 1; this allows the selectivity patterns for the different surveys to be presented on the same scale.

$$(1)\quad N_{a,y} = N_{a-1,y-1}\exp(-\{M + F_{a-1,y-1}\})$$

where $M$ is the natural mortality rate and $F_{a,y}$ is the fishing mortality rate for age $a$ fish in year $y$. For the 13+ category, numbers in each year after the first ($N_{13,y}$) were given by

$$(2)\quad N_{13,y} = N_{12,y-1}\exp(-\{M + F_{12,y-1}\}) + N_{13,y-1}\exp(-\{M + F_{13,y-1}\})$$

which were simply the survivors of the 13+ category plus the surviving 12-yr-olds from the previous year. Thus, numbers-at-age, excluding the initial age composition and recruitment each year, were not estimated as parameters, but instead were calculated from the initial age composition ($N_{a,1}$, $a$ = 6, ..., 13), recruitments ($N_{5,y}$, $y$ = 1, ..., 15), age- and year-specific fishing mortality rates ($F_{a,y}$, $a$ = 5, ..., 13; $y$ = 1, ..., 15), and the natural mortality rate ($M$).

$F_{a,y}$ was modeled as being separable:

$$(3)\quad F_{a,y} = F_y\, s_{f,a}$$

where $s_{f,a}$ was the fishery ($f$) selectivity on age $a$ fish and $F_y$ scaled overall fishing mortality in year $y$. In the model, $s_{f,10}$ was set equal to 1, so that $F_y$ equals $F_{10,y}$, the fishing mortality rate on age 10 fish in year $y$. A restriction of this type is necessary to parameterize uniquely the age and year effects (Doubleday 1976). We chose to normalize to selectivity at a constant age, rather than to the age of estimated maximum selectivity, as is often done, so that $F_y$ would have a constant definition. Thus, selectivity for some ages could exceed unity.

Age-group-specific fishery selectivity was assumed to follow a double-logistic function (Table 1; Fig. 1). The double-logistic

TABLE 1. Parameters and values used by the stock synthesis model (SSM) and by the simulation model. Some of these values were estimated by the SSM as formal parameters (E), others were assumed known (K), and others were determined by assumed constraints (C) (see text). Note that "known" values used for the SSM were the same as the values used in the simulations.

| Parameter | Description | Treatment by SSM | Values used by simulation |
|---|---|---|---|
| $F_y$ | Fishing mortality multiplier for year | C | From lognormal distribution with CV = 30% and mean of 0.075 or $0.30 \cdot yr^{-1}$ |
| $N_{5.y}$ | Recruitment at age 5 in year $y$ | E | From lognormal distribution; mean = 17.8$M$, variance = 110.3$M$ |
| $N_{a.1}$ | Initial numbers-at-age | E | Based on distribution for recruitment parameters |
| $\alpha_{f.i}$, $\beta_{f.i}$, $\alpha_{f.d}$, $\beta_{f.d}$ | Fishery selectivity parameters | E | −9, 1.46, 13.28, −1.14 |
| $\alpha_{s.i}$, $\beta_{s.i}$, $\alpha_{s.d}$, $\beta_{s.d}$ | Survey selectivity parameters | E | |
| | Recruit | | −1, 0.1, 14, −2.655 |
| | Dome-shaped | | −9, 1.46, 13.28, −1.14 |
| | Asymptotic | | −11.39, 2, 13.28, −0.001 |
| $q$ | Survey proportionality constant | C | 1 |
| $M$ | Natural mortality rate | K | $0.15 \cdot yr^{-1}$ |
| $\sigma_s$ | SD of log survey catch | K | Produces CV = 10, 25, or 50% |
| $\sigma_c$ | SD of log fishery catch | K | Produces CV = 1% |

function is flexible and can be used to model a wide variety of selectivity patterns, including nearly knife-edged, dome-shaped, and asymptotic (Methot 1990). This function is composed of two logistic functions, one increasing and the other decreasing. The product of the two logistic functions, after rescaling, was selectivity:

$$(4)\quad s_{f.a} = \frac{[1/\{1+\exp(-(\beta_{fi}\, a + \alpha_{fi})\}]\,[1/\{1+\exp(-(\beta_{fd}\, a + \alpha_{fd})\}]}{\lambda_{10}}$$

where $\alpha_{fi}$, $\alpha_{fd}$, $\beta_{fi}$, and $\beta_{fd}$ are the parameters of the increasing ($i$) and decreasing ($d$) logistic functions and $\lambda_{10}$ is equal to the value of the numerator of the equation for $a$ (age) = 10. $\alpha_{fi}$, $\alpha_{fd}$, $\beta_{fi}$, and $\beta_{fd}$ were estimated as formal parameters, while the overall scalers of fishing mortality, $F_y$, $y = 1, ..., 15$, were determined by constraints as described below. (Note that the selectivity of the 13+ group was assumed equal to the value predicted by equation 4 for $a = 13$.)

The last determinant of population dynamics was the natural mortality rate ($M$), which was fixed at a value of 0.15 based on prior information (Hightower and Lenarz 1986).

We now turn to how the synthesis model calculated its synthetic data to compare with observed data. We assumed that the observed data for each 15-yr period consisted of fishery age-composition data, total biomass of fishery catch during each year, annual survey age composition data from subsamples of the survey catch, and catch per unit effort (CPUE), a relative annual index of biomass available to the survey gear.

The numbers of each age caught by the fishery during each year were assumed by the synthesis model to follow the Baranov catch equations:

$$(5)\quad \eta_{f.a.y} = N_{a.y}\, F_{a.y}\, [1\text{-}\exp\{-M + F_{a.y})\}]/[M + F_{a.y}].$$

The synthesis model treated the fishery catch data as consisting of two independent pieces of information: (1) the proportion of the total numbers caught each year that fell into each age-group (i.e., the age-composition data), which were directly calculated from the $\eta_{f.a.y}$'s, and (2) the total biomass caught ($C_{f.y}$). Catch biomass was calculated simply as the sum over ages of the product of numbers caught at each age (from equation 5) and the weight at each age. The weight-at-age relationship was assumed to be known a priori, and equations developed by Lenarz (1987) and Phillips (1964) for widow rockfish were used to define this relationship.

Like the fishery catch data, the survey data were treated as containing two independent types of information for each year: (1) the proportions caught by the survey at each age (the age-composition data) and (2) a CPUE value representing an index of biomass available to the survey gear. The survey was assumed to have an insignificant effect on the stock size and to have occurred after recruitment for a given year, but before fishing or natural mortality. The synthesis model calculated the proportions-at-age caught by the survey in year $y$, the $P_{s.a.y}$'s, as proportional to the product of the model's current values for abundance of each age and the selectivity of the survey for the corresponding age ($s_{s.a}$):

$$(6)\quad P_{s.a.y} = s_{s.a} N_{a.y} / \Sigma_i\, s_{s.i} N_{i.y}\,.$$

In our application of the synthesis model, the survey selectivity pattern was defined by a double logistic function of age, just as the selectivity of the fishery was. The four parameters defining the function were estimated as formal parameters (Table 1). The CPUE index was fit by the synthesis model by assuming it to be proportional to the weighted (by selectivity) sum over ages of population weights-at-age. Population weight-at-age was simply the product of abundance-at-age $N_{a.y}$ and expected weight-at-age of an individual ($w_a$, assumed known as described above). Thus, the survey CPUE index in year $y$ was

$$(7)\quad C_{s.y} = q\Sigma_a\, w_a\, s_{s.a}\, N_{a.y}\,.$$

The proportionality constant $q$ was determined by a constraint as described below.

### Generation of Simulated Data

For each run, a new simulated data set was generated. All parameters defining the simulation model are given in Table 1, along with their values or the distribution from which they were generated.

The simulation model made essentially the same assumptions as were incorporated into the stock synthesis model described above. Given the initial age composition, recruitments, fishing mortality rates, and other (fixed) parameters (Table 1), we used equations 1–5 to simulate population dynamics and fishery catch over time. $M$ was fixed at 0.15, and the same set of fishery selectivity parameters (Table 1) was used in all cases, leading to a dome-shaped selectivity function (Fig. 1).

Each simulation run used randomly generated recruitments ($N_{5,y}$, $y = 1, \ldots, 15$), initial numbers at age ($N_{a,1}$, $a = 6, \ldots, 13$), and fishing mortalities ($F_y$, $y = 1, \ldots, 15$) in each year. Recruitment was generated from a lognormal distribution with specified mean and variance (Table 1, estimated from Hightower and Lenarz 1989). Initial numbers-at-age were calculated from randomly generated recruitment values, reduced for the cumulative natural mortality up to the age in question. As indicated above, this assumes insignificant fishing prior to the first year of the simulation. For age 13+, initial numbers were generated and summed for the youngest 50 year-classes in this age-group (numbers at older ages were negligible). Fishing mortality rate on age 10 fish ($F_y$), with the mean appropriate for the given set of runs, was generated from a lognormal distribution. The CV for $F_y$ was 30%, roughly approximating the variability in estimated fishing mortality seen in a number of different assessments of rockfish stocks (PFMC 1990). Note that the expected fishing mortality rate was constant over years and was not changed in response to the current estimate of the status of the stock.

In this model the expected level of recruitment was not a function of the biomass of the stock when the year-class was generated, and this implies that substantial compensation was taking place. The assumption was useful because direct effects of fishing on adult stock composition were not confounded with indirect effects on recruitment that would cause the average magnitude of recruitment to differ between low and high fishing mortality rates.

Both the fishery and survey age-composition data for each year were generated as multinomial samples with effective sizes of 400. The expected proportions-at-age were calculated directly from catch-at-age (equation 5) or by equation 6 (the survey). Some estimates of the variance of catch-at-age numbers for west coast groundfish suggest that our admittedly somewhat arbitrary choice of effective sample size (after Fournier and Archibald 1982) may not be unrealistic (Sen 1986; Methot 1990; Parker and MacCall, unpublished manuscript[2]). The total biomass caught by the fishery was assumed to be measured precisely, so observed catches were generated from a lognormal distribution with a CV of 1% about the true value, matching the error assumed by the assessment methodology in likelihood calculations (see below). The survey index of biomass was generated from a lognormal distribution with CV's of either 10, 25 or 50%, depending upon the particular run, and an expected value specific to the given year of the run. The expected index value was the sum of the products of expected survey catch-at-age and weight-at-age. The expected survey catch-at-age is given by numerator of equation 6, multiplied by $q$ (which was fixed at 1.0 for simplicity). We use the same weight-at-age relationship here as was assumed above in the synthesis model.

### Fitting the Synthesis Model to the Simulated Data Sets

For each run the numbers in age categories 6–13+ in the initial year ($N_{6,1}$–$N_{13,1}$), recruitment ($N_{5,1}$–$N_{5,15}$) in each year, four selectivity parameters for the fishery and four for the survey, $F_y$ in each year, and $q$ (the proportionality constant for the survey) were estimated. Of the above, the $F_y$'s and $q$ were determined by constraints, and the others are estimated as formal parameters. Other values used in generating synthetic data and calculating likelihoods either were constants assumed known a priori or were calculated from the formally estimated parameters, parameters determined by constraints, and the assumed constants.

As mentioned above, our estimates of $F_1$–$F_{15}$ and $q$ were obtained by requiring them to satisfy constraints. The $F_y$'s were continually updated along with the formal parameters so that the estimated catch biomass in each year exactly matched the observed catch, if this were possible (Methot 1990). A likelihood component for the catch biomass was included in the fitting so that solutions that did not allow the catch biomass to be matched (e.g., if an $F$ is fixed so that the population cannot support the observed catch) were penalized for this lack of fit through smaller likelihoods. Because the survey is a relative one, the survey proportionality constant, $q$, is chosen so that the sum of the model's estimated survey catches over years equals the observed sum based on the data (Methot 1990).

The set of formal parameter estimates and constrained values that maximized the log-likelihood function was chosen as the best fit (Fournier and Archibald 1982; Kimura 1990; Methot 1990). The log-likelihood ($L$) was

$$(8) \quad L = L_1 + L_2 + L_3 + L_4$$

where $L_1$ was the log-likelihood associated with the fit to the fishery age composition, $L_2$ was the log-likelihood associated with the fit to the survey age-composition data, $L_3$ was the log-likelihood associated with the biomass of fishery catch, and $L_4$ was the log-likelihood associated with the survey index of biomass. These individual components (ignoring constant terms) were

$$L_1 = \Sigma_y\, 400\, (\Sigma_a \tilde{P}_{f,a,y} \log \hat{P}_{f,a,y})$$

$$L_2 = \Sigma_y\, 400\, (\Sigma_a \tilde{P}_{s,a,y} \log \hat{P}_{s,a,y})$$

$$(9) \quad L_3 = \Sigma_y - 0.5 \left\{ \frac{\log\left(\dfrac{\hat{C}_{f,y}}{\tilde{C}_{f,y}}\right)}{\sigma_f} \right\}^2$$

$$L_4 = \Sigma_y - 0.5 \left\{ \frac{\log\left(\dfrac{\hat{C}_{s,y}}{\tilde{C}_{s,y}}\right)}{\sigma_s} \right\}^2$$

where a tilde indicates observed data and a circumflex indicates values estimated by the stock synthesis model. $P_{f,a,y}$ represents the proportion of the sample type $t$ (either fishery ($f$) or survey ($s$) in year $y$ that is age $a$, and $\sigma_t$ indicates the (assumed known) standard deviation on a log-scale of $\bar{C}^{t}_{y}$

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[2] K.R. Parker and A.D. MacCall. 1990. An interactive port sampling model for California groundfish. Administrative Report T-90-03, Tiburon Laboratory, 3150 Paradise Drive, Tiburon, CA.

$L_1$ and $L_2$, the log-likelihood components for the fishery and survey age compositions, reflect the assumption that the observed proportions-at-age for each year were produced as though the sampled fishery catch or sampled survey catch were multinomial samples of size 400. This "effective sample size" of 400 is internal to the likelihood component and acts to weight the magnitude of the component based upon the assumed precision associated with the sampling program. The value of 400 used here matched the actual sample size used to generate the age-composition data (see above). In practice, an analyst could estimate the effective sample size for each year based on independent information on the precision of the catch sampling program (Methot 1990). Our approach assumed that the effective sample size was constant, and more importantly, that it had been estimated correctly.

The likelihood components for the fishery catch biomass and the survey index were of lognormal form. Thus, the likelihood increased as the squared errors between the log-transformed observed and synthetic values decreased. The values of $\sigma_f$ and $\sigma_s$ were assumed known and act to weight the two components in the total log-likelihood. They were determined by the assumed level of error associated with each type of data. $\sigma_f$ was set at a value corresponding to a CV of 1% on the untransformed scale, which matches the level of error used to produce the observed (simulated) data. $\sigma_s$ was set at values corresponding to CV's of 10, 25, or 50% on the untransformed scale, with the level of error chosen to match the level of error used to produce the observed (simulated) data for the given run.

For interested readers, the next two subsections provide technical detail on the process of searching for the maximum likelihood solution.

### Numerical Details of the Fitting Procedure

The maximum likelihood solution was found using a Broyden–Fletcher–Goldfarv–Shanno update procedure combined with a cutback line search, a standard quasi-Newton method (Gill et al. 1981). Convergence was assumed when both the maximum change in any formal parameter value was less than 0.1% and the total log-likelihood changed less than 0.001%. Initial tests indicated that more stringent convergence criteria did not lead to improved estimates.

Our experience in fitting age-structured models to fishery data has indicated that results can be sensitive to initial parameter values, so we attempted to mimic the approach an analyst might use to specify initial values. Initial numbers at age and recruitment in each year were set by doing a cohort analysis (Pope 1972), following the approach used in Deriso et al.'s (1985) catch-at-age software (CAGEAN). Initial values for parameters determining fishery selectivity were set as follows. First, the $F_{a,y}$'s estimated by the cohort analysis were divided by $F_{y,10}$. These were then averaged over years to obtain an estimate of $s_{f,a}$ for each age, and the double-logistic function was fit to these estimates by least squares. The shape of the survey selectivity function was assumed to be essentially unknown, and a single set of initial values that produced a mildly dome-shaped selectivity function was used in all runs.

### Local versus Global Maxima on the Likelihood Surface

When maximizing a parameter-rich function, there is a real danger that a solution may only maximize the likelihood function locally. This is of special concern in simulation studies because it is generally not practical to simulate the critical review of a stock assessment scientist for each individual run. We found that the model occasionally converged to solutions that did not have the global maximum likelihood. We discovered this by first noting that in some cases the estimated fishery selectivity function was asymptotic, or more rarely flat or decreasing, instead of the correct dome-shape. In a separate set of runs, we examined whether these solutions were true maximum likelihood solutions by fixing the fishery selectivity parameters at the correct values and reestimated the remaining parameters. Cases that originally estimated either a flat or declining fishery selectivity curve showed a substantial increase in the likelihood function, while likelihoods were similar to original values for cases where the original estimated fishery selectivity was either dome-shaped or asymptotic. In some test cases, we did not have success reaching the true maximum likelihood solution by restarting the fitting process from the incorrect solution.

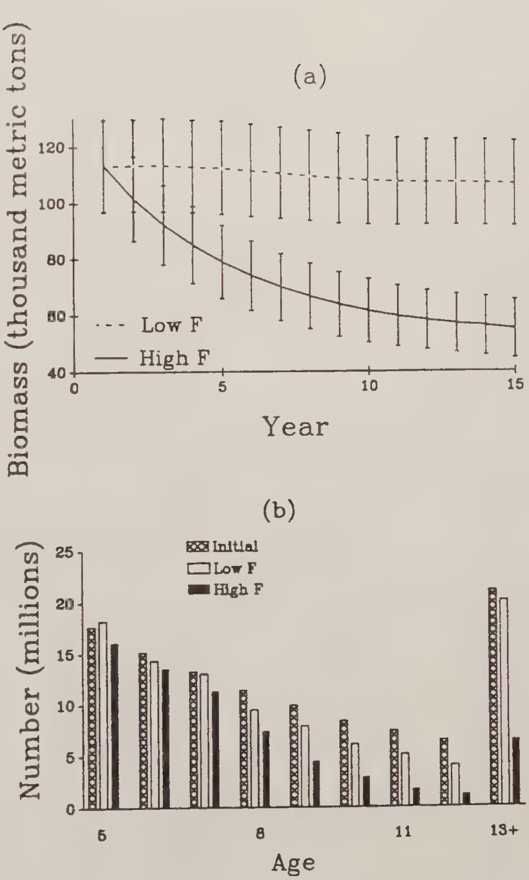

FIG. 2. True population dynamics of simulated populations. (a) Average biomass (± SD) plotted against time for high and low fishing mortality rates and (b) average initial and final numbers-at-age for low and high fishing mortality rates.

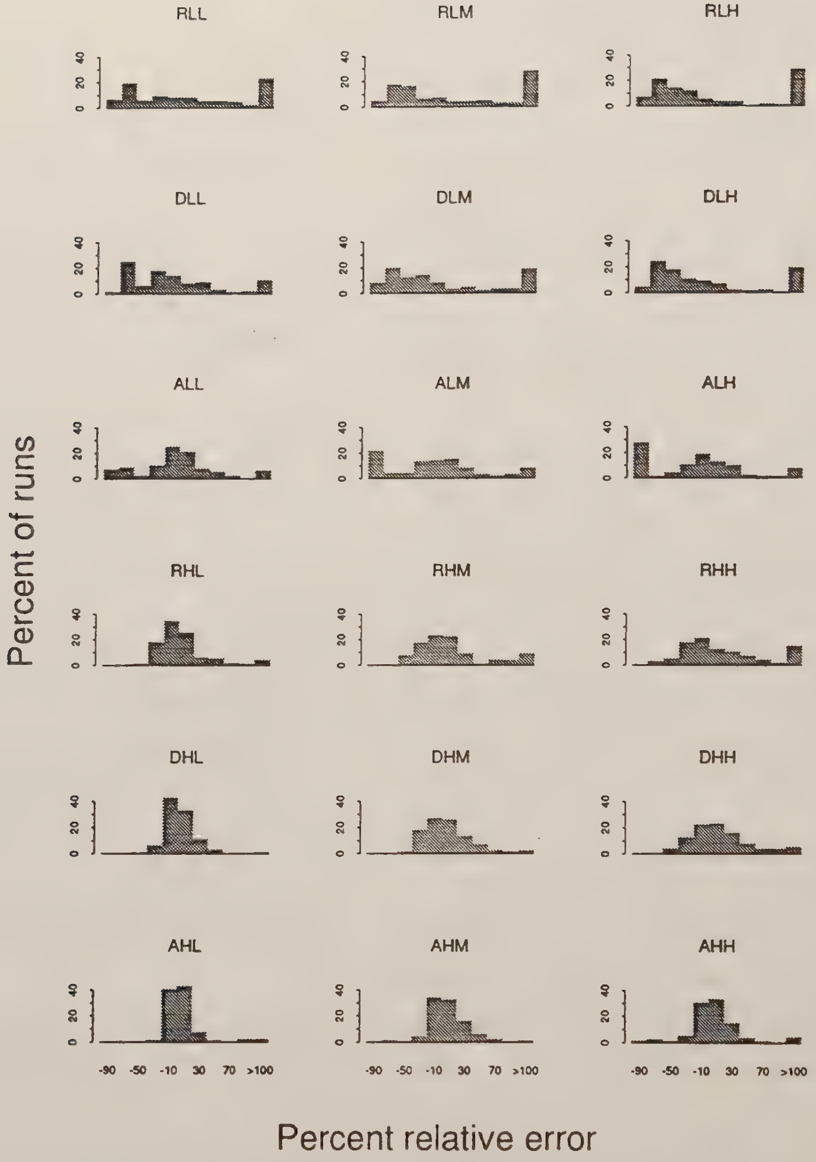

FIG. 3. Distributions of relative errors in estimated year 15 biomass for each case. Headings of the form "XYZ" denote the survey selectivity (X = R, D, or A for recruit, dome-shaped, or asymptotic, respectively), the fishing mortality rate (Y = L for low ($0.075 \cdot yr^{-1}$) or Y = H for high ($0.3 \cdot yr^{-1}$), and the survey coefficient of variation (Z = L, M, or H for low (10%), medium (25%), or high (50%), respectively) for each case.

In real assessments, we expect that declining or flat selectivity curves would be considered suspect, and additional runs would be done with different initial values for the parameters, so that a solution close to the maximum likelihood might be found. A real analyst might also run the stock synthesis model with a grid of starting values and potentially avoid the problem we encountered in the cases described above. We have therefore excluded runs that, by inspection, would be categorized as nearly flat or generally declining. (We defined as nearly flat or declining any case where the estimated fishery selectivity for age- 5 fish was greater than 70% of the maximum estimated selectivity; this is substantially above the true selectivity at age 5, which is 17% of the maximum, and nearly all values over 25% were also over 70%.) Because of the rarity of the "flat" and declining estimated curves (about 5% of the runs), excluding these runs does not influence any of our qualitative con-

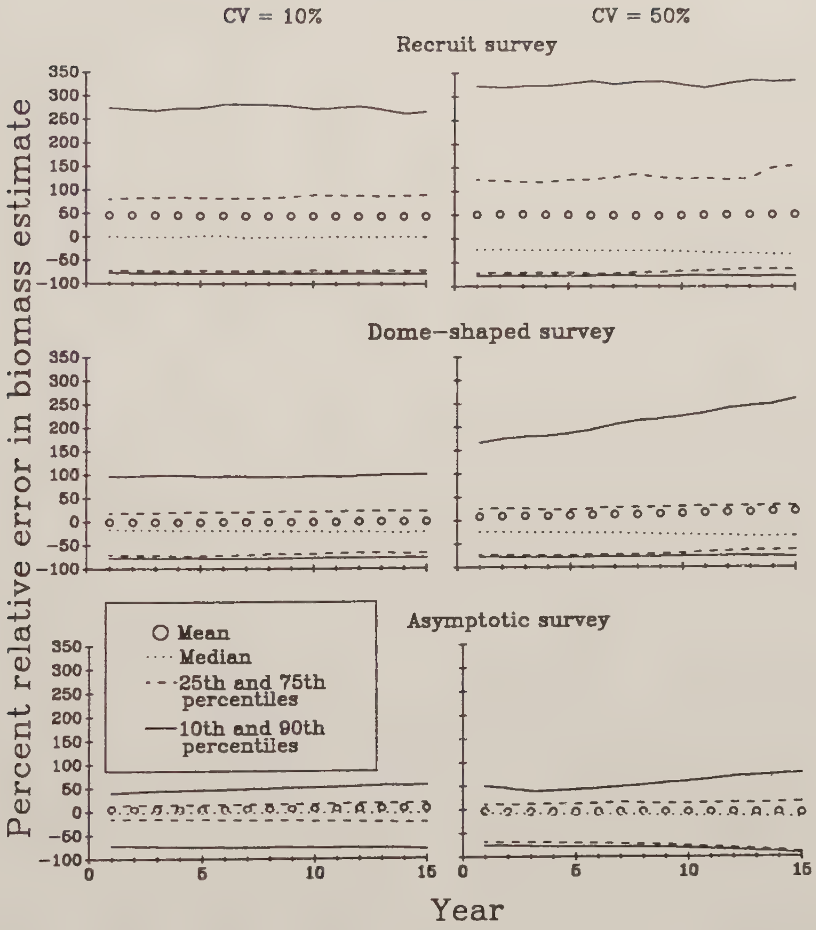

FIG. 4. Relative error in biomass estimates plotted aginst year for the low fishing mortality rate. Shown are results for survey CV's of 10 and 50%. For conciseness, results for survey CV's of 25% are not displayed; they were intermediate between the displayed cases.

TABLE 2. Percentage of runs with estimates of year 15 biomass within 20% of the correct value.

| Survey type | Fishing mortality | Survey variability | | |
|---|---|---|---|---|
| | | Low | Medium | High |
| Recruit | Low | 16.8 | 11.8 | 8.8 |
| | High | 60.6 | 46.1 | 33.7 |
| Dome-shaped | Low | 22.6 | 12.0 | 16.2 |
| | High | 76.0 | 53.0 | 45.5 |
| Asymptotic | Low | 46.2 | 29.2 | 32.0 |
| | High | 84.2 | 66.5 | 64.0 |

clusions. If included, these runs would accentuate the patterns presented below because the cases with the most variable results also produced more estimated flat and declining selectivity functions, and runs with these erroneous selectivity patterns also tended to have large errors in other parameters.

## Results

### Population Dynamics

Under the high fishing rate scenario, average biomass fell by about half from year 1 to 15, and the contribution of the older ages, particularly the 13+ category, declined markedly (Fig. 2). On average, biomass leveled off in the final years of the simulations because the population was coming into balance with the higher mortality imposed by fishing. Under the lower fishing rate, the decline in biomass was only slight, and the shift in the age distribution was not marked.

### Skewed Distribution of Errors

We examined the distributions of percent relative error (PRE) = 100 × (estimated-true)/true for each run both for biomass and recruitment estimates. For each type of survey the distribution of errors was skewed, so that the mean PRE typically exceeded the median (Fig. 3–7). Median errors were typically

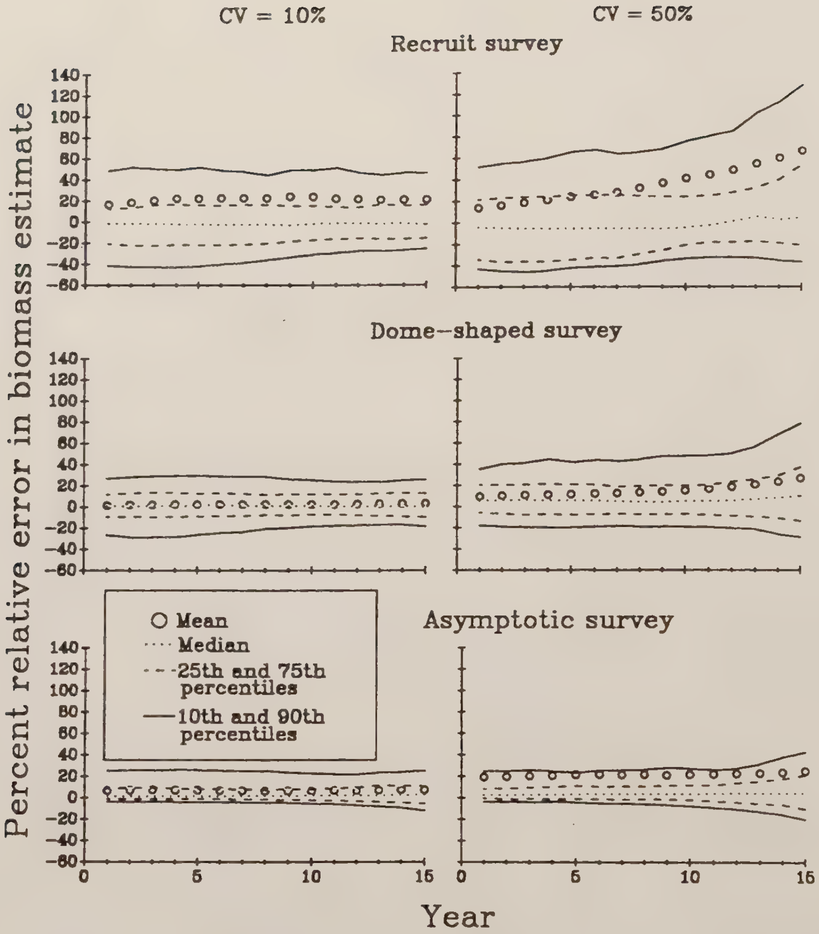

FIG. 5. Relative error in biomass estimates plotted against year for the high fishing mortality rate. Shown are results for survey CV's of 10 and 50%. For conciseness, results for survey CV's of 25% are not displayed; they were intermediate between the displayed cases.

close to zero. Given the variability in the magnitude of errors and the skew of the distributions, it was clear that the mean error alone would sometimes be an insufficient measure of the performance of the stock synthesis model.

### Accuracy and Precision in Biomass and Recruitment Estimates

For management purposes, the accuracy of biomass estimates in the final year of an assessment is usually of greatest interest. Consequently, we examined the distribution of relative errors in estimated biomass in the 15th year (Fig. 3) and also tabulated the percentage of runs with year 15 biomass estimates within 20% of the correct value (Table 2). Although 20% is a somewhat arbitrary cutoff, we felt that stock assessments with errors less than 20% would be classified as successful by most workers. The overall pattern in the results is for greater accuracy and precision given a higher fishing mortality level and when survey precision was higher (Table 2; Fig. 3). Errors were most concentrated around zero for the asymptotic survey and least concentrated around zero for the recruit survey (Table 2; Fig. 3). The difference in accuracy and precision between the recruit and asymptotic surveys was comparable with differences within a survey type when its CV ranged from 10 to 50%. The difference between the asymptotic and dome-shaped surveys was accentuated at a low fishing rate (Table 2; Fig. 3). This latter result is reasonable because the asymptotic survey sampled older fish to a greater extent, and these constituted a larger proportion of the year 15 stock at a low fishing rate (Fig. 2).

Estimates of biomass and recruitment in earlier years are also of interest because they can provide information on how the stock is changing over time. In general, the precision and accuracy of biomass (Fig. 4 and 5) and recruitment (Fig. 6 and 7) estimates over the entire time series showed the same qualitative patterns as year 15 biomass estimates. The most accurate and precise estimates came from the asymptotic survey and the least accurate and precise from the recruit survey. As might be

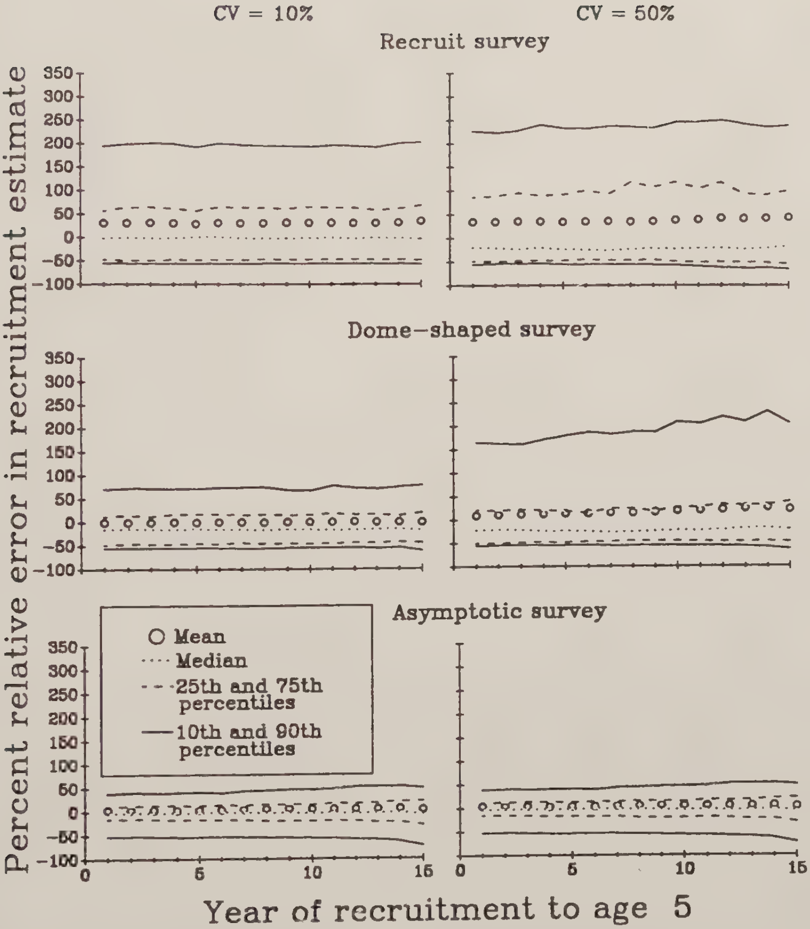

Fig. 6. Relative error in recruitment estimates plotted against year for the low fishing mortality rate. Shown are results for survey CV's of 10 and 50%. For conciseness, results for survey CV's of 25% are not displayed; they were intermediate between the displayed cases.

expected, estimates were better when the survey CV was lower or the fishing mortality rate was higher.

Errors in estimated biomass in year 15 were generally associated with an overall scaling error. These scaling errors caused the correlation between errors in biomass estimates and errors in initial number and recruitment parameter estimates to be high, although the correlations did fall off some at the beginning and end of the time series (Fig. 8). The correlation between errors in recruitment (or initial numbers-at-age) and errors in year 15 biomass estimates tended to be weakest in cases where absolute estimates of biomass were best. For example, correlations were generally lower at the higher fishing mortality rate, especially for the dome-shaped and asymptotic surveys with a CV of 10%.

To the extent that errors were due to an overall scaling problem, estimates of relative year-class strength might still be quite good even when absolute estimates were poor. We measured relative recruitment, on a log scale, as log-transformed recruitment minus the mean of log-transformed recruitment. Estimated and true values of relative recruitment were highly correlated (Fig. 9). Although lower, the correlations were still substantial even at the end of the time series. The lowest correlations were for the dome-shaped survey at the end of the time series of recruitment estimates. This is not unexpected because these year-classes were never well sampled by this survey.

Substantial errors in year 15 biomass were sometimes associated with trends in estimated recruitment, as estimated by linear regression of recruitment estimates against year. Stong trends were most evident when the fishing mortality rate was low, especially when final biomass was substantially overestimated (Fig. 10). For this case, although more trends were positive, some strong trends were negative, and in these cases, biomass in the first year was overestimated to an even greater degree than year 15 biomass. Strong trends were less common at the higher fishing mortality rate, and underestimates tended to have more declining trends and overestimates more increasing trends (Fig. 10).

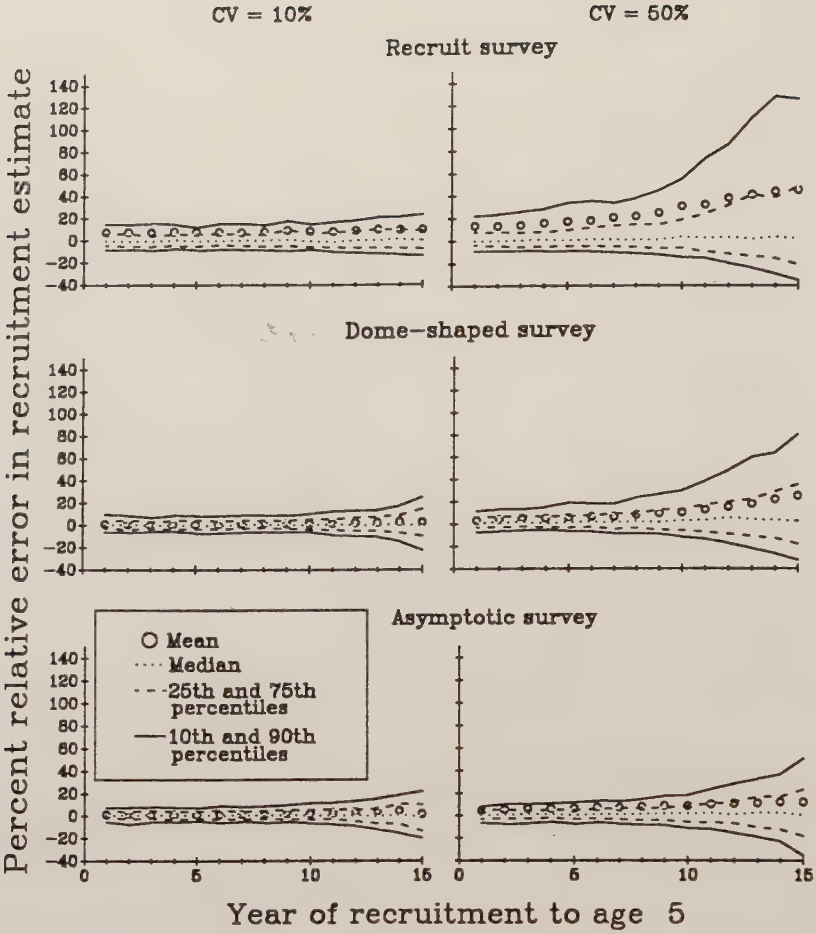

FIG. 7. Relative error in recruitment estimates plotted against year for the high fishing mortality rate. Shown are results for survey CV's of 10 and 50%. For conciseness, results for survey CV's of 25% are not displayed; they were intermediate between the displayed cases.

### Temporal Patterns in Biomass and Recruitment Estimates

By analogy with cohort analysis, it is reasonable to expect convergence of estimated values of recruitment as we move back in time, with the convergence being stronger at higher fishing mortality rates (Pope 1972). To the extent that the convergence property carries over to separable models, and the convergence is toward the true value, we would expect to see tighter distributions of relative errors in estimated recruitment earlier in the time series and at higher fishing mortality rates. Our results match this expectation. At the lower level of fishing mortality, there appears to have been only slight convergence in earlier years toward the correct value of recruitment (Fig. 6). In contrast with the low fishing rate results, there was substantial convergence for estimates of recruitment at the high level of fishing mortality (Fig. 7).

In a number of cases, biomass estimates improved as we moved backward in time (Fig. 4 and 5). This, however, is not a general result. For example, at a high fishing mortality level with a low-variability dome-shaped survey, the most accurate biomass estimates are in year 10, with slightly less accurate estimates in earlier years (Fig. 5). This may have occurred because some of the cohorts contributing to biomass in the early years were observed only for a few years before moving into the 13+ category (see also Kimura 1989).

## Discussion

In this paper, we used Monte Carlo simulation to evaluate the performace of the stock synthesis model. Our study was unique in its assessment of the value of a relative survey (i.e., one proportional to available stock, but with the proportionality constant unknown) to the synthesis model, and especially in the comparison of such surveys with different selectivity patterns. Although we only examined the stock synthesis model in our simulations, we suspect that many of our results apply more generally to statistically based catch-at-age methods such as

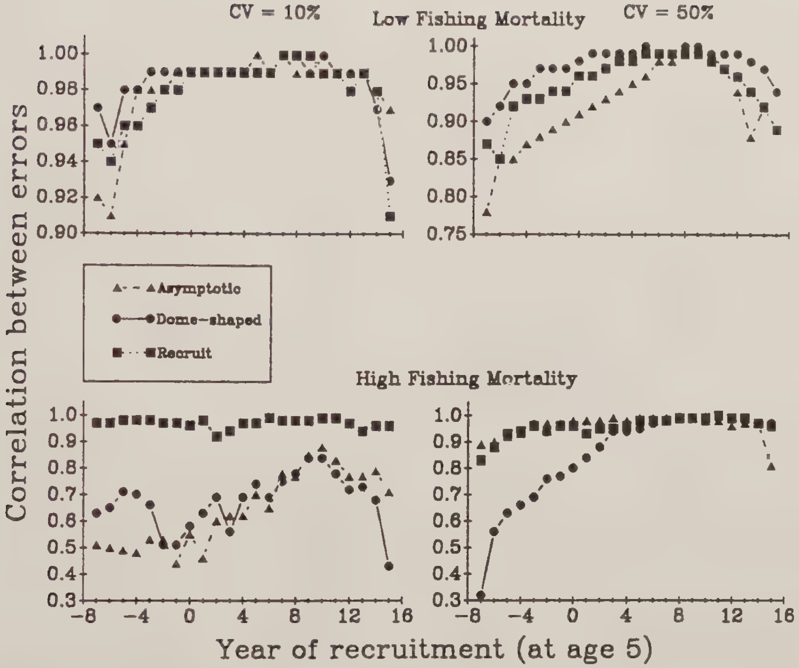

FIG. 8. Correlation between relative error in estimated biomass in year 15 and relative error in estimates of initial numbers-at-age and recruitment parameters. Correlation is plotted against the year of recruitment to age 5 associated with the parameter. Thus, the correlations with recruitment parameters ($N_{5,y}$, $y = 1, ..., 15$) are plotted at $X$ values of $y = 1, ..., 15$, and the correlations with initial numbers-at-age ($N_{a,1}$, $a = 6, ..., 13$) are plotted at $X$ values of $a - 6 = 0, -1, ..., -7$. For example, the correlation between the relative error in estimated year 15 biomass and initial numbers at age 8 ($N_{8,1}$) is plotted at an $X$ value of $-2$ because age 8 fish in year 1 recruited at age 5 3 yr earlier. For conciseness, results for survey CV's of 25% are not displayed; they were similar to displayed results.

CAGEAN (Deriso et al. 1985) and perhaps also to tuned virtual population analysis (e.g., Pope and Shepherd 1985). Care should be taken in extrapolating from our results to short-lived species because the role of survey selectivity could be quite different when the population is composed of only a few age-classes.

Although tangential to the main thrust of this paper, we think that it is of interest that the synthesis estimates of recruitment and biomass were generally positively biased. In contrast with the mean errors, median errors were generally quite close to zero. This kind of "transformation bias" is a well-known phenomenon arising from the skew in the lognormal distribution of errors we assumed. We suspect that such a bias is built into many catch-at-age methods and is probably a real phenomenon because in practice, most distributions of errors will be skewed. However, whether a median or mean error of zero (or something else) is desired depends in part upon management goals (see also Pope and Shepherd 1985).

In our study, an asymptotic survey was best for estimating current stock size within some fixed percentage of the correct value. Accuracy fell some for the dome-shaped survey, and the recruit survey produced estimates that were considerably less accurate than those associated with the other survey types. These results suggest that, all else being equal, an asymptotic survey should be chosen. The extent, however, to which the selectivity pattern of a survey can be controlled or chosen is of pragmatic concern. For example, fish behavior, distribution, and ability to avoid capture may make it difficult to design an asymptotic survey. However, a combination of surveys that together capture a broad range of ages may provide many of the benefits we have associated with an asymptotic survey. In the end, choices among survey types will involve their relative costs, the value of forecasting future recruitment (e.g., Walters 1989), as well as the expected accuracy of the resulting estimates of current biomass. When these trade-offs are being made, it is important to keep in mind that differences in the performance of surveys with different selectivity patterns can be quite substantial, rivaling differences in performance resulting from severalfold differences in coefficients of variation in survey error.

A relative survey can be used to help determine absolute abundance primarily because it provides information on how the fished stock changes from year to year. The magnitude of these relative changes can then be related to the absolute magnitude of the fishery catch. The poor performance associated with the recruit survey can be understood by noting that most fish captured by the recruit survey have not yet experienced fishing mortality. Thus, changes in survey CPUE reflect year-to-year variations in relative recruitment, but are largely uncoupled from changes in the stock due to fishing. Furthermore, the

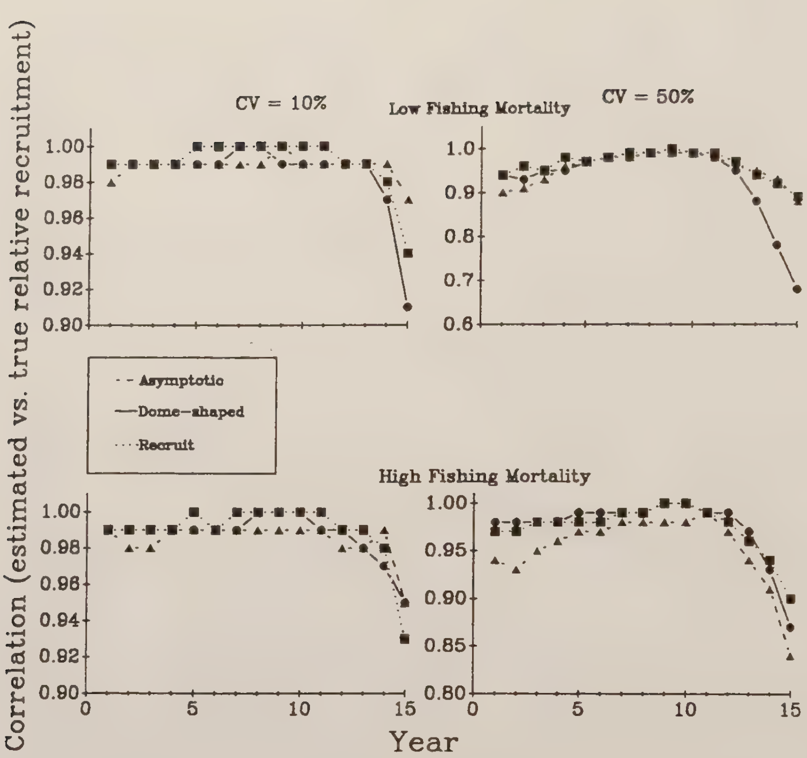

FIG. 9. Correlation between estimated relative recruitment and actual relative recruitment plotted against the year of recruitment. For conciseness, results for survey CV's of 25% are not displayed; they were similar to displayed results.

fishery age-composition data alone already contain substantial information on relative year-class strength (e.g., Ricker 1975, p. 265–272), but essentially none on absolute stock size (Doubleday 1976; Deriso et al. 1985; Shepherd and Nicholson 1986). Consequently, much of the information on relative year-class strength provided by the recruit survey is redundant and does not provide information on absolute abundance. Indeed, for the recruit survey, our stock synthesis estimates of relative recruitment were quite good, even though absolute estimates of recruitment and biomass tended to have large errors.

When fishing mortality has been low, assessments of current stock size based on fishery catch-at-age data and a survey of relative abundance will often be substantially in error. Under higher cumulative fishing mortality, it is intuitive that catch-at-age analyses give better results because such a large proportion of each cohort of fish are counted in the catches (Pope 1972). However, our results suggest that even when $F$ is high, the relative survey must be highly precise to have a high probability that an estimate of current abundance will be within 20% of the correct value. Although large errors in estimated year 15 biomass were sometimes associated with incorrect patterns for the fishery selectivity function in our study, most of the estimated patterns were not "pathological," and we doubt that an analyst could rule them out as unreasonable without making use of information external to the assessment. With a very long time series, a relative survey might fix absolute abundance adequately, even at a low fishing mortality rate, but then the assumptions of constant natural mortality, selectivity patterns, growth, etc., are probably untenable (e.g., Walters 1986).

We believe that our simulation study presents a best-case scenario for stock assessments. In the simulations, selectivity or weight-at-age did not change over time, natural mortality was assumed known and remained constant (over years and ages) at the assumed value, and catch biomass was assumed to be known accurately. The precision of our simulated survey varied from high (CV = 10%) to modest (CV = 50%), and we assumed that there was a survey every year. In practice, the real population will deviate from the synthesis (or other) model to an unknown extent, and the quality and quantity of data will often be lower than in our simulations.

To place our simulations in context, it is worth considering the actual kinds of data usually available for use with the stock synthesis model. Assessments of several groundfish stocks on the west coast of North America make use of trawl survey data collected every third year with CV's near 50% (Bence and Rogers 1992; Rogers and Bence 1992). For many stocks, natural mortality was estimated by catch curves, maximum ages, or simply by analogy with other species (e.g., Hightower and Lenarz 1986; Bence and Rogers 1992; Rogers and Bence 1992). In our simulations, we generated data with a very low level of sampling error for catch biomass because this is the assumption under which the synthesis model is fit to the data. However, we recognize that catch biomass estimates are probably less accurate than the low level of error built into our simulations

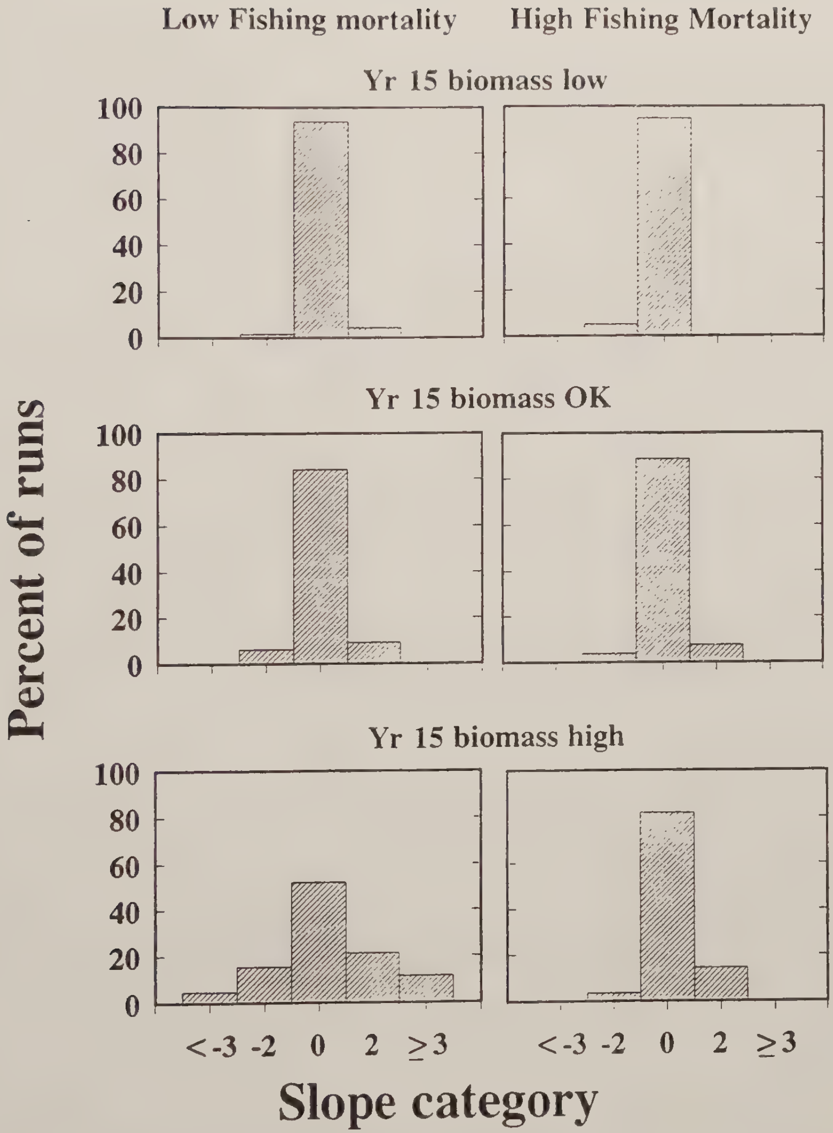

FIG. 10. Distribution of estimated slopes (by linear regression) of the trend in estimated recruitment over time. Distributions were calculated separately for replicates with low (more than 20% low), OK (within 20% of the correct value), or high (more than 20% high) estimates of year 15 biomass. Shown are results for an example low and high fishing mortality case (dome-shaped selectivity, CV = 25%); other cases showed similar patterns.

because of two general problems. First, discard levels generally are estimated roughly from an observer program of restricted spatial and temporal extent. Thus, even when landings are made in nearly pure "market categories" and reported landings are essentially a census of the landed catch, as they are for widow rockfish, the error in catch biomass could be substantial. Second, estimation of landed catch is complicated for some stocks because landings are made in mixed-species market categories that need to be sampled (Bence and Rogers 1992). This can sometimes cause the estimates of landings to have substantial sampling error. For most assessments using the synthesis model, age-composition data appear to be quite good, at least as representations of the landed catch. Estimated proportions at age in the landed catch often come from extensive sampling at the ports (stratified both spatially and by time of year) combined with the reading of thousands of otoliths.

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# Hatch Dates and Growth of *Ommastrephes bartramii* Paralarvae from Hawaiian Waters as Determined from Statolith Analysis

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**Abstract:** Planktonic young (paralarvae) of *Ommastrephes bartramii*, have recently been found in early spring (March-May) along the Hawaiian Archipelago. Statoliths of paralarvae ($N = 57$) sampled in February 1991 were used to estimate ages, hatch dates, and growth rates. Growth increments within statoliths were enumerated using light and scanning electron microscopy. Under the assumption that increments were formed daily, paralarvae were estimated to grow exponentially for at least 35 days post-hatching. Based on the growth model, paralarvae 15, 25, and 35 days old had estimated mantle lengths of 1.6, 4.3, and 12.1 mm, respectively. The paralarvae were estimated to have hatched between 1 and 25 January 1991, based on back calculation of statolith increments from the time of capture.

## Introduction

Events occurring during the early life history of squids may profoundly influence their recruitment, for squids are presumably most susceptible to natural mortality during embryonic and paralarval development. The dominant sources of natural mortality in the early life history of marine fishes, and presumably squids, are a combination of density-dependent factors, such as starvation (Lasker, 1975) and predation (Houde, 1987), and density-independent factors, such as temperature and oceanic transport to unfavorable areas (Bailey, 1981; Parrish *et al.*, 1981). Recruitment may be especially influenced by paralarval growth rates which may determine the duration of the paralarval stage: Small declines in paralarval growth rates could result in a longer planktonic period during which high mortality rates are presumed to operate.

Daily growth increments in squid statoliths provide a method for precisely determining the ages, growth rates, and hatch dates of squid from the field. Increment counts have been used to estimate the ages of several squid species and life history stages (see review by Rodhouse and Hatfield, 1990). The daily nature of growth increments has been verified, through laboratory studies, to occur in a variety of teuthoid and sepioid species (e.g., Dawe *et al.*, 1985; Lipiński, 1986; Yang *et al.*, 1986; Jackson, 1989; Nakamura and Sakurai, 1990; Bigelow, 1992), although the physiological mechanisms responsible for increment formation remain obscure (Morris, 1988) Estimation of hatch dates, back calculated from ages at the time of collection, can define periods of successful spawning. Spawning sites may be identified from hatch dates in conjunction with physical data on the rate and direction of ocean currents.

*Ommastrephes bartramii*, is an abundant squid in the subtropical-temperate Pacific Ocean. Since the reduction in stocks of the squid *Todarodes pacificus* in the early 1970's, North Pacific stocks of *O. bartramii* have been targeted by a Japanese jig fishery and by an international driftnet fishery composed of fishermen from Japan, Korea, and Taiwan. Japan's annual catch of *O. bartramii* ranged from 100,000 to 215,000 metric tons between 1981 and 1989, with approximately 80% of the catches taken by the squid driftnet fishery (Murata, 1990; Yatsu *et al.*, in press).

Growth of *O. bartramii* has been estimated from analysis of length-frequency distributions of sequential samples from the jig and driftnet fisheries (e.g., Murakami *et al.*, 1981; Murata *et al.*, 1988). These studies suggest that North Pacific populations are composed of winter and spring cohorts, with a life span of approximately 12–18 months for females and 12 months for males.

*Ommastrephes bartramii* paralarvae are known to occur in two geographical areas: southeast of Honshu, Japan (ca. 35°N, 140°W: Okutani, 1968; 1969), and along the Hawaiian Archipelago (Hayase, 1989; Young and Hirota, 1990). Paralarvae occur in waters off Japan during January, March, April, and May (Okutani, 1968, 1969) and in waters off the Hawaiian Archipelago from at least February to May (Hayase, 1989; Young and Hirota, 1990; R.E. Young pers. comm.). Vertical distribution data suggest that *O. bartramii* paralarvae typically occur at the surface and at 0–40m depth during day and night (Okutani, 1968; Young and Hirota 1990).

Our study examined the growth increments within statoliths of field-caught *O. bartramii* paralarvae (2.1 to 13.7 mm mantle length (ML)) from Hawaiian waters. Using age and hatch-date estimates based on enumeration of growth increments, we estimated paralarval growth rates, defined the periods of successful spawning, and drew inferences about the duration of the paralarval period.

## Materials and Methods

### *Paralarval collections*

*Ommastrephes bartramii* paralarvae were collected during synoptic plankton surveys within 100 nmi of the Hawaiian Archipelago in February 1991 with the NOAA ship *Townsend Cromwell* and the Hokkaido University ship *Hokusei-Maru*. Sampling gear consisted of a 4-$m^2$ ring net, 0.8-$m^2$ ring net, and a Manta neuston net (0.49-$m^2$ mouth)—all with 505 $\mu$m mesh. Oblique tows to approximately 100m were taken with the 4-$m^2$ ring net, and surface tows were taken with the 0.8-$m^2$ ring and Manta nets (Table 1). Paralarval squid were sorted from the plankton on board ship with stereomicroscopes; they were immediately fixed in 95% ethyl alcohol or 99% isopropyl alcohol. Mixed layer temperatures were obtained at each station from conductivity-temperature-depth casts to 1,000m or expendable bathythermograph casts to 700m.

### *Laboratory procedures*

Paralarvae from four locations were used for statolith examination (Table 1). Paralarval identifications followed Young and Hirota (1990) and were confirmed by R. E. Young (University of Hawaii). Dorsal ML and proboscis length of each paralarva was measured to the nearest 0.1 mm with an ocular micrometer and a stereomicroscope. Both statoliths were extracted from the paralarva and placed on microscope slides, then rinsed with distilled water and allowed to dry. Statoliths were mounted in clear resin (Eukitt or Petra-epoxy) with the anterior (concave) side positioned upward. The terminology of Clarke (1978) and Lipinski *et al.* (1991) are used to describe statolith external features and microstructures. Statolith dimensions of focus-dorsal dome length, focus-rostral length, and total length between the dorsal dome and rostrum were measured with an ocular micrometer and compound microscope to the nearest 2 $\mu$m. Microstructural examinations were made with a research-quality compound microscope with transmitted light at magnifications of 600–1500×. Whole statoliths from small ($\leq$6 mm ML) paralarvae were viewed with no further preparation, while statoliths from large (>6 mm ML) paralarvae were ground and polished prior to microscopy to improve increment resolution. Grinding was done by hand rubbing the embedded statolith against fine-grained (1200 grit) sandpaper. The statolith was then polished with 0.3 $\mu$m alumina-silica polishing powder.

For some paralarvae, one statolith of the pair was examined with scanning electron microscopy (SEM) to validate observations made with light microscopy. The lateral dome was ground until the focus was at the ground surface. The surface was polished, etched with 0.1% EDTA for 5–20 minutes, and coated with gold in a vacuum evaporator. Statolith microstructures were viewed and photographed with a Hitachi S-800 SEM at various magnifications (700–5,000×).

An increment under light microscopy consisted of a wide, light ring and a narrow, dark ring, while

**Table 1.** Data on samples of *Ommastrephes bartramii* paralarvae captured and aged from waters around the Hawaiian Archipelago in February 1991.

| Station | Date | Time | Lat. (N) | Long. (W) | Gear | Depth (m) | Temperature (°C) | N | Mantle length (mm) |
|---|---|---|---|---|---|---|---|---|---|
| A1 | 7 Feb | 1553 | 21°56.0′ | 166°52.7′ | 4-$m^2$ ring | 0–100 | 23.8 | 3 | 3.6–4.7 |
| A2 | 7 Feb | 1903 | 21°55.7′ | 167°07.4′ | Manta | 0–1 | 23.8 | 5 | 6.1–13.7 |
| B | 8 Feb | 0930 | 23°04.3′ | 158°57.5′ | 0.8-$m^2$ ring | 0–2 | 22.6 | 36 | 2.1–4.4 |
| C | 13 Feb | 1907 | 25°04.4′ | 163°06.7′ | 4-$m^2$ ring | 0–100 | 21.4 | 6 | 2.8–5.0 |
| D | 15 Feb | 1904 | 23°11.3′ | 161°54.1′ | 4-$m^2$ ring | 0–90 | 23.1 | 7 | 6.5–8.3 |

an increment under SEM. appeared as a wide, lightly etched area (light ring) and a narrow, deeply etched area (dark ring). For each microscopy method, statolith increment counts were made independently by each author at four separate reading sessions.

## Results

Microstructural examination revealed a conspicuous, dark, elliptical zone in the interior of all statoliths under light and SEM (Figs. 1–3). Under SEM, the long axis of the ellipse averaged 21.8 $\mu$m (SD = 3.4 $\mu$m, $N = 17$), while the short axis averaged 17.4 $\mu$m (SD = 2.8 $\mu$m, $N = 17$). This distinctive zone was postulated to be the statolith size at hatching or natal size, because of the similarity in size to *Illex illecebrosus* (Balch *et al.*, 1988) and *Abralia trigonura* (Bigelow, 1992). In the microstructural examination, two features influenced increment enumeration. Weak increments were present between more typical increments on the dorsal dome in a zone of progressively increasing increment width. Increments bordered by distinct, deeply etched, dark rings were presumed to be daily (Fig. 4A), while subdaily increments were defined by faint, shallowly etched, dark rings (Fig. 4B). A second feature influencing increment enumeration was about a 10- to 15-$\mu$m area, immediately distal to the natal ring, that lacked any consistent structuring (Fig. 3). As a matter of convention, increments were enumerated based on continuity of increment width with adjacent increments. The magnitude of the count bias associated with unresolved growth increments appeared to be small, because increment widths of 3-4.5 $\mu$m were extrapolated over an unresolved area of 10–15 $\mu$m. Interpretation of the remainder of the statolith was largely unambiguous. In both microscopy methods, increments were always enumerated from the natal ring to the lateral dome (Figs. 1–2), as statolith orientation was not sufficient to allow increment counts on the rostrum or dorsal dome.

Statoliths were examined with light microscopy from 57 paralarvae of 2.1–13.7 mm ML. A paired $t$-test showed a significant difference between the mean increment counts of the two readers ($p < 0.05$). Mean difference between readers was 2.6 increments. For both readers, no significant difference was found between mean counts of paired statoliths from the 47 paralarvae in which both statoliths were extracted (one-way analysis of variance, $p > 0.05$).

Statoliths from 24 paralarvae were examined with SEM. Mean difference between readers was 0.9 increments. Contrary to mean increment counts from light microscopy, there was no significant differ-

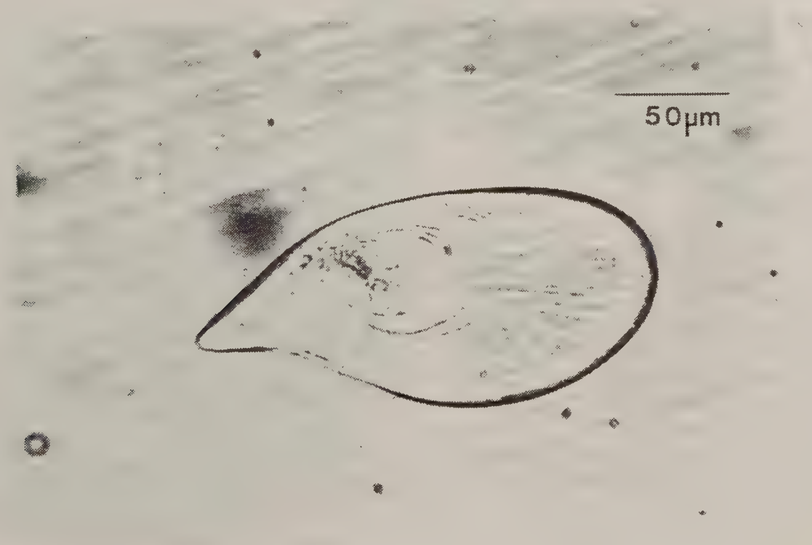

**Fig. 1.** *Ommastrephes bartramii.* Light micrograph of a statolith from a 2.5 mm mantle length paralarva used for increment enumeration.

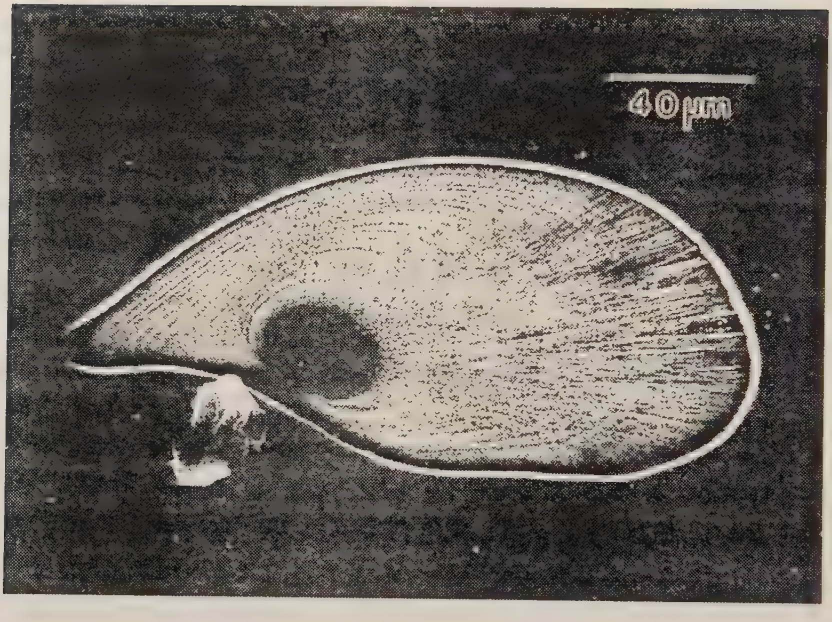

**Fig. 2.** *Ommastrephes bartramii.* Scanning electron micrograph of a ground and etched statolith from a 2.5 mm mantle length paralarva used for increment enumeration.

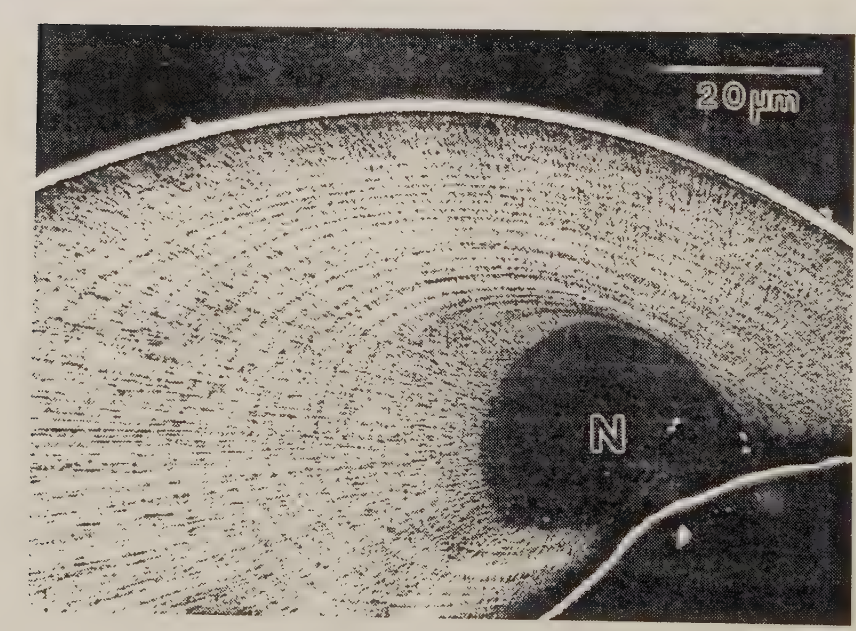

**Fig. 3.** *Ommastrephes bartramii.* Scanning electron micrograph of a ground and etched statolith from a 5.0 mm mantle length paralarva, which demonstrated a nucleus (N).

ence between mean SEM counts of the two readers ($p > 0.05$). No significant difference was found between pooled increment counts from light microscopy and SEM ($p > 0.05$). Differences in increment counts between readers were greater with light microscopy compared to SEM, because under light microscopy, microstructures around the natal zone were difficult to resolve and subdaily increments were more prominent.

For each paralarva, increment counts of both readers made with light microscopy were averaged for analysis of growth in length. An increase in squid size and increment number resulted in an increase in all statolith dimensions (Fig. 5A-B). Increment at length data were pooled over all stations and the following exponential model was fit to the data:

$$ML = 0.331e^{(0.103x)}$$

where ML is in millimeters and $x$ equals the mean increment count (Fig. 6). Nonlinear regression parameters were estimated by least-squares methods. Coefficient of determination ($r^2$) was 0.92. Deviations from the model included individual variability in growth of a paralarva, error in ML measurements, and error in increment counting. Residuals exhibited no conspicuous systematic deviation from linearity by sampling site and no marked increase in variance with age. There were too few samples to test for differences in growth rates between stations. Based on the growth model, paralarvae at an age of 15 days post-hatching (1.6 mm ML) grew at a rate of 0.16 mm·day$^{-1}$, whereas the growth rate of 35-day-old paralarvae (12.1 mm ML) was 1.25 mm·day$^{-1}$ (Table 2). Paralarval length at time of hatching was estimated to be 0.33 mm ML.

The proboscis of *O. bartramii* started dividing by about 6 mm ML (Fig. 7). Proboscis division was completed between 9.5 and 12.0 mm ML, which corresponds to an age range of 32–35 days.

Hatch dates were back calculated through the subtraction of the paralarval age from the date of collection, and were pooled into 3-day periods (Fig. 8). Samples were not pooled because paralarvae were collected with different net types over a large geographical area. The hatching period was 1–25 January 1991. At stations B, C, and D, paralarval hatch dates occurred over a narrow range of 8 days, while paralarvae sampled at station A hatched over a period of 16 days. Paralarvae collected at stations B and D had similar hatch dates (12–19 January 1991).

## Discussion

Analysis of statolith microstructures allowed us to realistically estimate the growth and hatch dates of

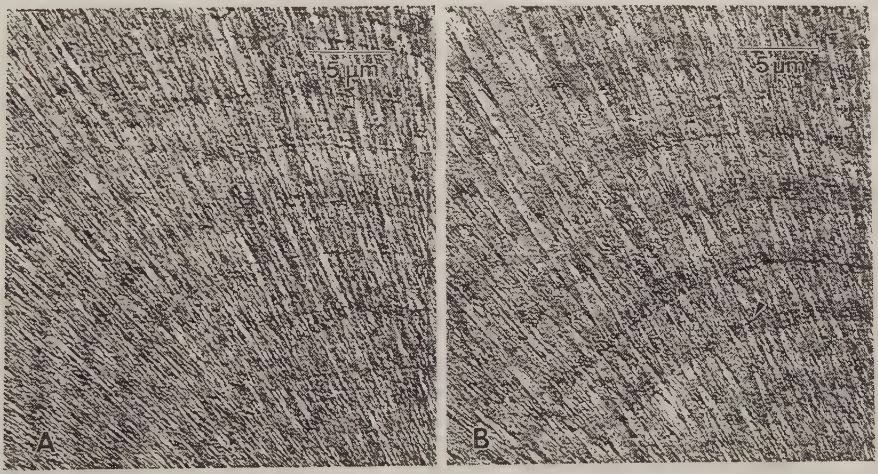

**Fig. 4.** *Ommastrephes bartramii.* Scanning electron micrograph of increments within a statolith. (A) Daily increments were bordered by deeply etched, dark rings. (B) Subdaily increments were composed of faint, shallowly etched, dark rings (arrow).

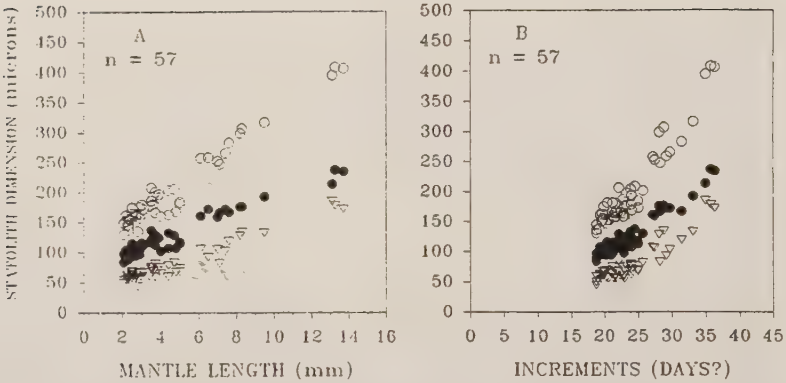

**Fig. 5.** *Ommastrephes bartramii.* Relationship between (A) statolith dimensions and mantle length of paralarvae, and (B) statolith dimensions and number of growth increments (open circles indicate statolith total length; closed circles, focus-dorsal dome length; and triangles, focus-rostral length).

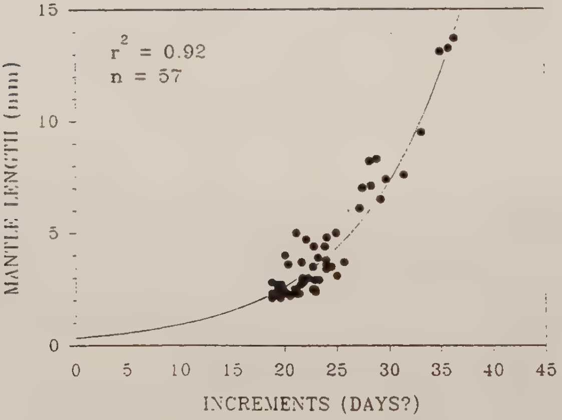

**Fig. 6.** *Ommastrephes bartramii.* Relationship between mantle length and number of increments in statoliths. Exponential growth curve was based on increment counts from statoliths of 57 specimens viewed with light microscopy.

*O. bartramii* paralarvae. A primary assumption of statolith microstructural analysis is that growth increments are formed daily. Growth increments of *O. bartramii* paralarvae are assumed to be daily, based on the similarity in increment appearance in previous studies that validated the frequency of increment deposition (e.g., Dawe *et al.*, 1985; Bigelow, 1992). Validation experiments are impossible at present because eggs, presumably laid in masses, have never been captured and field-caught individuals are not amenable to statolith marking experiments for they perish quickly in captivity. Although we did not validate the frequency of increment deposition, previous studies have for two orders of cephalopods (Teuthoidea and Sepioidea) (e.g., Dawe *et al.*, 1985; Lipiński, 1986; Yang *et al.*, 1986; Jackson, 1989; Nakamura and Sakurai, 1990; Bigelow, 1992), which suggests that daily increment formation may be common to many cephalopod species. However, the existence of subdaily increments in *O. bartramii* statoliths and other squids (Jackson, 1990; Bigelow, 1992) may be a potential source of error if im-

**Table 2.** Comparison of paralarval growth in mantle length (ML) of three ommastrephids based on presumed daily growth increments within statoliths

| | Age | | | | | |
|---|---|---|---|---|---|---|
| | Day 15 | | Day 25 | | Day 35 | |
| | Size ML (mm) | Growth (mm/day) | Size ML (mm) | Growth (mm/day) | Size ML (mm) | Growth (mm/day) |
| *Ommastrephes bartramii*[a] | 1.6 | 0.16 | 4.3 | 0.45 | 12.1 | 1.25 |
| *Illex illecebrosus*[b] | 1.8 | 0.08 | 2.7 | 0.11 | 4.2 | 0.17 |
| *Stenoteuthis oualaniensis*[c] | 2.4 | 0.08 | 3.4 | 0.11 | 4.8 | 0.16 |

[a] From the present study; [b] From Balch *et al.* (1988); [c] From Bigelow (1991).

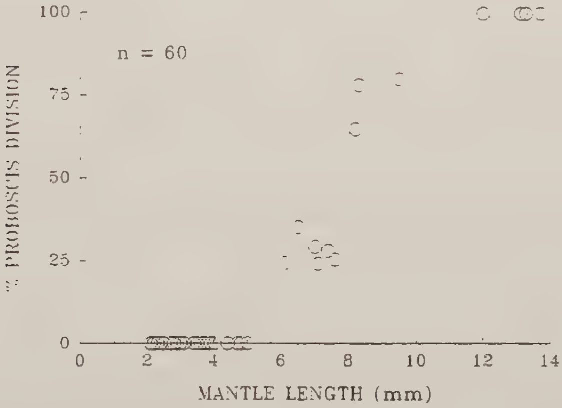

**Fig. 7.** *Ommastrephes bartramii.* State of proboscis division by mantle length.

properly interpreted. A second source of error in interpretation is the presence of an area immediately distal to the natal zone which lacked any consistent structure. Difficulty in resolving increments near the natal ring has been documented for a number of squid species (e.g., Dawe *et al.*, 1985; Jackson, 1989; Bigelow, 1991). Presumably, this ambiguous area corresponds to the yolk stage within early life history. Cues for increment deposition, such as feeding cycles, may not be as strong in the yolk stage and may result in poorly defined increments.

Paralarval growth in length of various squids typically conforms to exponential equations (e.g., Balch *et al.*, 1988; Forsythe and Hanlon, 1989; Bigelow, 1991). Paralarval growth in length of *O. bartramii* is also characterized as exponential for at least 35 days post-hatching. The derived estimate of hatching size (0.33 mm ML) from the growth model is probably underestimated. Although the hatching size of *O. bartramii* is unknown, the size may be approximately 1 mm ML, because other confamilial species are known to hatch at this size [*Todarodes pacificus*, 1.2 mm ML (Hayashi, 1960); *Illex illecebrosus*, 1.2 mm ML (O'Dor *et al.*, 1982)], and Young and Hirota (1990) captured a yolk-stage paralarva which was approximately 1.0 mm ML. In the future, smaller (1–2 mm ML) paralarvae may be captured, and age at length estimates may provide a model which extrapolates to a realistic estimate of ML at hatching.

Our paralarval growth rates are comparable to growth estimates of confamilial species. Paralarval growth derived from statolith analysis has been estimated for *I. illecebrosus* captured from the Gulf Stream off Florida (Balch *et al.*, 1988) and *Stenoteuthis oualaniensis* from Hawaiian waters (Bigelow,

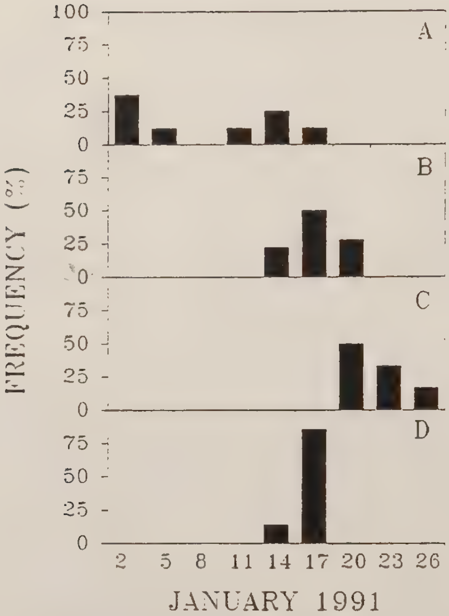

**Fig. 8.** *Ommastrephes bartramii.* Hatch-date distributions derived from examination of statolith microstructures. Stations A, B, C, and D correspond to collection sites in Table 1.

1991). The ML at age estimates were modeled for the three species (Table 2). Though temperature and food effects are unknown, *O. bartramii* paralarvae grew the fastest, while *I. illecebrosus* and *S. oualaniensis* paralarvae grew at similar rates. Since temperature can affect paralarval growth rates (Forsythe and Hanlon, 1989), an age- and temperature-based growth model similar to that recently developed for fish larvae (Campana and Hurley, 1989) could be applied in future comparisons of paralarval growth rates.

The paralarval stage of the Ommastrephid family is classically considered to end with the division of the proboscis to separate the tentacles and is therefore referred to as the rhynchoteuthion stage. A change in statolith growth axes has been postulated to coincide with a transition in life history stages of some squid (Morris and Aldrich, 1985; Bigelow, 1992). For *I. illecebrosus*, the splitting of the proboscis is complete by 8–10 mm ML (O'Dor, 1983). Based on a change in statolith form at about 50 mm ML, Morris and Aldrich (1985) suggested that the paralarval stage extends beyond the rhynchoteuthion stage in *I. illecebrosus*. For *O. bartramii*, the division of the proboscis is complete at 9.5–12.0 mm ML, though there was no change in statolith dimensions at the end of the rhynchoteuthion stage. Therefore, we concur with Morris and Aldrich (1985) in suggesting that the paralarval stage of *O. bartramii* may extend beyond the rhynchoteuthion stage.

The ages of *O. bartramii* paralarvae in our study indicate a hatching period between 1 and 25 January. *Ommastrephes bartramii* paralarvae (6–8 mm ML) have been captured from Hawaiian waters as late as 5 May (Hayase, 1989). Assuming a growth rate similar to the present study, the paralarvae sampled by Hayase (1989) would have hatched between 5 and 7 April. The apparently protracted spawning period concurs with present theories (see review by Murata, 1990) that North Pacific stocks of *O. bartramii* are composed of cohorts spawned during winter and spring.

Statolith analyses are invaluable to ecological and population studies, as they supply the cephalopod biologist with a technique to resolve life history information on a daily level. Future studies with larger sample sizes of *O. bartramii* paralarvae may reveal the environmental conditions which are favorable for paralarval growth and survival.

## Acknowledgements

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# Fisheries and Marine Resources of Hawaii and the U.S.-associated Pacific Islands: An Introduction

GEORGE W. BOEHLERT

## Introduction

Fisheries of Hawaii and the U.S. insular Pacific are quite different from typical industrial and recreational fisheries of the mainland U.S. Fisheries productivity in coastal waters of these tropical and subtropical islands may be similar to that in temperate continental shelf-slope fish communities (Marten and Polovina, 1982), but the higher species diversity results in more diverse, lower volume fisheries. Larger, commercial fisheries are often dependent upon deep water, slope-dwelling species or the highly migratory pelagics such as tunas and billfishes. Although land masses in this region are small, the U.S. Exclusive Economic Zone (EEZ) surrounding the island areas is immense, covering over 2 million square miles. Over this broad geographic expanse, a variety of cultural differences affect fishing practices, and even those practices present today are significantly different from the native approaches to fishing methods in Hawaii (Smith, 1993) and Guam (Hensley and Sherwood, 1993). Finally, variations in the population size and in the fishing pressure on the nearshore ecosystem are marked among islands, from the highly populated island of Oahu in Hawaii to sparsely populated islands elsewhere to the mostly uninhabited islands of the Northwestern Hawaiian Islands (NWHI) and Commonwealth of the Northern Mariana Islands (CNMI).

The objective of this volume is to describe our current knowledge on the varied fisheries of Hawaii and the U.S.-associated islands of the Pacific. This introductory paper provides some general background on fisheries in the region.

## Diversity of Fisheries

In the U.S. insular Pacific, the combination of highly complex habitats, high species diversity, and both native and newly introduced cultural practices leads to a diversity of fisheries unparalleled in most other parts of the U.S. Many fisheries are unique to certain localities, such as that for palolo worm in American Samoa (Craig et. al., 1993), seasonal juvenile fisheries for rabbitfish in Guam (Hensley and Sherwood, 1993), and limpet, or opihi fisheries in Hawaii (Smith, 1993). Others are common to all islands, such as the seasonal fisheries for juvenile bigeye scad in all areas. The adults of these coastal pelagics, known as akule in Hawaii or atule in American Samoa, represent the largest volume fishery in nearshore waters but are poorly known in terms of their resource potential. Nearshore reef resources are often overexploited in populated areas, a problem perhaps characteristic of tropical reef fisheries in general (Ferry and Kohler, 1987).

## Evolution of Fisheries

With increasing population, changing cultural composition, and advancing technology, island fisheries have changed in many ways. Prior to western colonization, indigenous peoples of the islands depended on the marine environment and had developed a unique knowledge of marine resources and varied approaches to conservation and management. The cultural impacts of colonization of the islands by non-indigenous peoples had marked effects and typically led to the decline of traditional conservation measures (Johannes, 1978); a concise description of how this happened in Belau, in the Western Caroline Islands, is provided by Johannes (1981). In Guam, Spanish persecution of Chammorros led to the demise of the traditional fishing methods in the mid-1500's (Hensley and Sherwood, 1993). Similarly, in Hawaii, it led to the decline of the traditional management regime of the native Hawaiians that had long protected nearshore resources (Smith, 1993). Trends in the fisheries of Hawaii are perhaps the most pertinent to examine, for the greatest changes have occurred there and these may serve as a warning of what may come in the other island areas as populations increase there as well.

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*ABSTRACT — The fisheries of Hawaii and other U.S.-associated islands in the Pacific Ocean are characterized by high diversity, both in the species exploited and the human cultures that exploit them. The commercial sector has undergone rapid growth in recent years, but recreational and subsistence sectors remain important. Information on these fisheries is generally not available in published form. This paper presents an overview and introduction to a volume of papers describing fisheries in the region, with the goal of making the information available to scientists and the general public. A great deal remains to be learned about the dynamics of these fisheries as well as the associated issues in biological research, fisheries management, and environmental protection.*

Temporal trends of fisheries differ markedly. Shomura[1] described the differences in fisheries of Hawaii between 1900 and 1986, the early period based upon a comprehensive data collection scheme and subsequent analysis by Cobb (1902) and the later period upon State of Hawaii commercial fishery data collection systems. While the two data sets are not identical in coverage, they provide useful comparisons. The total catch nearly doubled in the period considered. Shomura[1] noted several important trends related to the distance of the fishery from shore. Catch of coastal species declined by about 80%, while those of neritic-pelagics (akule, opelu) declined by 40%. Catch of slope and seamount species increased by 80%, whereas manyfold increases in offshore pelagics catch were evident.

It is likely that the decline of nearshore fisheries is based largely upon two factors. First, increasing population and improved fishing technology led to overfishing in the absence of effective management and regulations. Gillnet use, for example, is largely unrestricted, and this can have negative impacts on coral reef fish populations (Gobert, 1992). Similar concerns are expressed about this gear in Guam (Hensley and Sherwood, 1993). Second, habitat destruction from coastal development leads to a decline in availability and quality of critical habitat area needed to support the reef populations. This was most evident for species utilizing fishponds, a habitat which may be similar to estuaries for enhancing juvenile fish production. The decline of the numbers and function of fishponds in Hawaii has been dramatic. Cobb (1902) documented the use of fishponds in his survey of fisheries of Hawaii and even then noted a marked decline in the numbers of functioning fishponds. While the reasons may differ, declining nearshore catches in American Samoa over the last two decades (Craig et al., 1993) are also a concern.

Significant growth in several fishery sectors of Hawaii has been based upon improved technology and an expanded potential geographic range of fishing. The combination of increased catch and targeted high-value markets led to a doubling of the ex-vessel value of Hawaii fisheries from 1970 to 1990 (Pooley, 1993a). Insular fisheries moved to increasingly deeper water, and technology allowed the expansion of the slope fishery in the main Hawaiian islands during the middle of this century. As these fisheries approached full exploitation, the resource potential of the NWHI was examined by the National Marine Fisheries Service, the State of Hawaii, and the U.S. Fish and Wildlife Service in the tripartite Northwestern Hawaiian Islands Investigation in the mid 1970's to early 1980's. This program increased knowledge of resource potential (Uchida and Uchiyama, 1986) and ultimately led to a geographic expansion of the lobster and bottomfish fisheries to the NWHI (Polovina, 1993; Haight et al., 1993), providing a marked expansion of exploitable biomass. Within the NWHI lobster fishery, changing gear from wire to plastic traps led to significant catch of slipper lobster, which had been essentially unexploited with wire traps. As these resources become fully exploited, however, the available habitat for further expansion of insular fisheries in Hawaii declined markedly.

The pelagic fisheries sector has seen the most dramatic fluctuation in Hawaii. Improvement of vessel technology increased the range of the local trolling and handline fleet while other factors led to the near-demise of the skipjack pole-and-line ("aku") fleet; with the closure of the only cannery on Oahu, recent aku catches are nearly an order of magnitude below the historical peak (Boggs and Kikkawa, 1993). A general trend away from "bulk fisheries" for pelagics (e.g. fishcake, canned tuna) and development of "quality," high price products (e.g. sashimi tuna, transshipped products) has enhanced the market value of Hawaii's pelagic fisheries (Pooley, 1993b). Even so, continuing improvements in technology have led to substantial expansion of the longline fishery and more directed targeting for bigeye tuna and broadbill swordfish fishery during the late 1980's (Boggs and Ito, 1993).

## Management Issues

With the decline of traditional management approaches, increasing population, and development of new fisheries, declines in nearshore stocks were inevitable (Shomura[1]; Hensley and Sherwood, 1993). As offshore fisheries grew, allocation conflicts have developed (Boggs and Ito, 1993). With the passage of the Magnuson Fishery Conservation and Management Act of 1976 (MFCMA) and establishment of the regional fishery management councils, federal jurisdiction was established and in some cases established regulations that superseded state or territory regulations. As the Western Pacific Regional Fishery Management Council (WPRFMC) began to develop fishery management plans (FMP's), the lack of adequate fisheries data became evident. Although time series of fisheries catch information were available in the state of Hawaii, questions existed about the quality and consistency of these data for rigorous analysis (Smith, 1993). Data for Hawaii's recreational fisheries, which may represent a large portion of harvest in the nearshore areas, are virtually unrecorded. In Guam, American Samoa, and CNMI, however, de novo development of the WPACFIN system began consistent time series of fisheries data (Hamm, 1993).

Management mechanisms have evolved in Hawaii to reduce fishing effort in the commercial fisheries, including limited entry (bottomfish, lobster), moratoria on new entrants to the fishery (longlining), closed seasons and quota (lobster), and area closures (longlining). Nearshore areas in Hawaii have received limited protection through Marine Life Conservation Districts (MLCD's), a progressive approach taken by the Division of Aquatic Resources (Smith, 1993). Such closed areas for fishery management purposes represent an alternative that is consistent with interest in marine refuges and sanctuaries, and a theoretical basis for such management is developing (DeMartini, 1993). Closed areas have also been used for special purposes, such as creating areas for nonconsumptive use of marine resources (a function served by many Hawaii MLCD's) or for protection of sensitive areas. An example of the latter is protection of the Hawaiian monk seal in the NWHI (Nitta and Henderson, 1993). Lobster fishing is prohibited inside 10 fm in the NWHI owing to designation of critical habitat for the monk seal, and longlining is prohibited within 50 n.mi. of the NWHI owing to fishery interactions.

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[1] R. S. Shomura. 1987. Hawaii's marine fishery resources: Yesterday (1900) and today (1986). Honolulu Lab., Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Cent. Admin. Rep. H-87-21, 25 p.

Interactions among different scales of fisheries and the differing agencies responsible for their management present a challenge in many areas. In the nearshore, non-selective gears like gillnets and lack of data on their catch make specific management measures difficult and contribute to stock declines. Moving offshore, many stocks, such as bottomfish, fall within the jurisdiction of both state (or territory) and federal management prerogatives; this problem is presently being faced with bottomfish management in the main Hawaiian Islands. For pelagics, even though all species are now under the MFCMA, fluctuations in catch rates of many species mimic many of the changes in Pacific-wide stocks, suggesting that local fluctuations are in concert with the wider Pacific stocks, and that local effects often change with environmental variation. Unfortunately, the wider ranging stocks lack the scientific basis and institutional structures needed for management (see Doulman, 1987).

## Environmental Issues

Improved awareness of environmental issues in the marine environment is evident in the general public, and Hawaii and the Pacific islands are no exception. Land-based development associated with increasing population in island ecosystems is a serious concern owing to degradation of nearshore habitats (Boehlert et al.[2]; Baines and Morrison, 1990). Examples of problems include point and nonpoint source pollution, coastal landfills, diversion of freshwater from former estuarine areas or fishponds, dredging and siltation impacts on corals, and algal blooms. While such problems may not be evident in all these island areas, their relationship to human population pressure is well documented.

Fishing can itself impact the environment; destructive fishing practices (bleach, dynamite, or nonselective gears) have a long history in island areas, but public awareness has led to regulations banning or controlling them. Set gillnet fishing is increasingly viewed as a nonselective method with relatively high bycatch of unintended species, similar to driftnet fisheries. In Hawaii, however, bills to regulate set gillnets have routinely been killed politically, although a recent (1992) resolution calling for studies to improve regulations was passed.

Impacts of fishing on protected species is also a point of environmental concern. Examples in local fisheries include gillnet impacts on turtle, and longline takes of turtles, monk seal, and seabirds (Nitta and Henderson, 1993).

Fishing may also have impacts on biological diversity. Fishing only selected species in the high diversity ecosystems characterizing these areas may lead to species replacement, and the new dominant species may be smaller and less useful for human consumption (Jones, 1982). While concrete documentation of such species replacement is not evident in Hawaii and the U.S. insular Pacific fisheries, experimental fishing on patch reefs at Midway did change community structure and the abundance of certain prey species (Schroeder, 1989). A more dramatic example is provided by the trawl fishery in the Gulf of Thailand, where the dominant fish and large invertebrate species decreased to less than one-fifth of their original abundance (as reflected in catch rate), and the squid *Loligo* spp. became the clear dominant, with perhaps a ten-fold increase in abundance (Longhurst and Pauly, 1987). Multispecies management models for tropical fisheries are not sufficiently well developed to predict these kind of changes (Sainsbury, 1982).

## Concluding Remarks

The papers in this volume document the development of this region's fisheries and indicate the scope of research that has been conducted by many agencies; still, it is clear that much remains to be learned. This is also true for the fisheries management and environmental protection issues as for the basic biological and environmental research required to understand the physical processes at work in these diverse island habitats. For successful fisheries management, however, it is critical to appreciate the human diversity of these island areas; this requires a deeper understanding of the social processes which affect the ability of government to work with the community on common solutions to fishery management problems. I hope that this volume contributes the basic background information which can place the search for such solutions on a firmer scientific footing.

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# ICHTHYOPLANKTON ASSEMBLAGES AT SEAMOUNTS AND OCEANIC ISLANDS

*G. W. Boehlert and B. C. Mundy*

## ABSTRACT

Seamounts and oceanic islands support demersal or neritic fish populations and are localized sources of eggs and larvae added to a background of oceanic ichthyoplankton. Associated larval fish assemblages, however, have been identified in few studies, and most have been based on subjective classifications of species by reproductive characteristics. At seamounts, little evidence exists that ichthyoplankton assemblages differ from the background field despite physical mechanisms proposed to maintain planktonic forms. Larvae of bottom-associated species are notably rare in samples taken in these regions. In contrast, characteristic ichthyoplankton assemblages have been described at oceanic islands. Unique assemblages may exist in embayments and lagoons, but they are not well described. Nearshore assemblages (0 to 0.5 km offshore) are dominated by larvae of small species with demersal eggs; neritic assemblages (0.5 to 5 km offshore) include inshore species with demersal and planktonic eggs mixed with larvae of certain species that are usually oceanic as adults. Although larvae of some inshore species with pelagic eggs are found offshore in oceanic assemblages (beyond 3 to 5 km), assemblages there are poorly described. Spatial and seasonal spawning behavior of adults plays the key role in formation of ichthyoplankton assemblages. Mechanisms that may maintain ichthyoplankton assemblages at islands include boundary layers, small scale frontal dynamics, tidal currents, topographically produced eddies, seasonally reduced or variable currents, and regions of no or returning flow. Behavior of larvae, particularly that affecting vertical distribution, can modify the influences of these mechanisms. The integrity of assemblages can be disrupted by both biotic and abiotic factors.

Seamounts and isolated oceanic islands are habitats for demersal and pelagic fish communities not found in the open ocean. These communities are point sources of eggs and larvae that contribute to ichthyoplankton assemblages of the surrounding oceanic waters. Recruitment back to seamounts and islands depends upon the fate of the egg and larval stages and thus, to some extent, upon their retention near these habitats. Distance from these isolated habitats is therefore an important variable in consideration of such assemblages.

The unique problem that seamounts and oceanic islands pose to the recruitment of fishes was first stated by Gosline and Brock (1960): ". . . the possibility presents itself that variations in the normal pattern of oceanic currents around the islands may sweep a variable number of these young fish with their relatively feeble swimming abilities beyond the point of no return." They also suggested, "This argues that the migratory pattern of these fishes is uniquely adapted to best assure their return to the inshore habitat at the proper time." Their suggestions have since formed the basis of the hypotheses investigated by most studies of ichthyoplankton in island areas.

The factors affecting the existence of ichthyoplankton assemblages may be conveniently classified into those influencing formation, maintenance, or disruption (Table 1). The formation of assemblages is influenced not only by adult spawning patterns, but also by current-topography interactions that may accumulate buoyant plankton (Miller, 1974; Wolanski et al., 1989; Black and Moran 1991). Optimal physical and biotic conditions may also lead to species associations (e.g., "ecological safe sites"; Frank and Leggett, 1983). Maintenance of larval fish assemblages involves an increasing role of larval fish behavior, including seeking specific environmental features (Sulkin, 1986; Olla and Davis, 1990), and prey-

Table 1. Factors of potential importance in the formation, maintenance, and disruption of ichthyoplankton assemblages around islands and seamounts

| Type of factor | Influencing formation* | Influencing maintenance† | Influencing disruption‡ |
|---|---|---|---|
| Adult behavior | Spawning location<br>Spawning time (tidal, diel, lunar, seasonal) | None | Predation (cannibalism)<br>Influences on settlement |
| Egg development | Buoyancy (demersal vs. pelagic eggs, egg density)<br>Incubation time<br>Hatching location<br>Hatching time | None | None |
| Larval behavior | Buoyancy at hatching<br>Swimming ability at hatching | Habitat preference (temperature, salinity, light, depth)<br>Vertical migration | Ontogenetic changes in vertical distribution<br>Metamorphosis (settlement, schooling) |
| Biotic environment | Predation (absence will create "ecological safe sites") | Prey presence | Predation<br>Prey absence (starvation) |
| Abiotic environment | Convergences<br>Fronts | Eddies (Taylor Columns)<br>Upwelling<br>Downwelling<br>Internal waves<br>Convergences<br>Fronts | Diffusion<br>Mixing<br>Advection |

* Factors promoting spatial and temporal co-occurrence.
† Factors promoting integrity of assemblages over time.
‡ Factors causing eventual breakdown of assemblage structure.

searching behavior (Hunter and Thomas, 1974; Doherty et al., 1985). Behavioral interaction with hydrography may result in dramatic accumulations of larvae into very localized assemblages (Kingsford, 1990). Because islands and seamounts may also be the loci of enhanced primary productivity (Doty and Oguri, 1956; Genin and Boehlert, 1985), retention near these areas may confer an advantage in survival.

In opposition to the factors forming and maintaining ichthyoplankton assemblages are those disrupting them. Mixing from turbulent flow, wind events, or other features will disrupt assemblages and dilute them over time. Advection may retain an assemblage intact, but can alter its position relative to a fixed sampling point, and thus its detection. Changes in larval behavior with ontogeny may alter the assemblage composition over time. Finally, the end of participation in an assemblage may be considered the point at which juveniles leave the environment occupied by larvae.

Investigations of ichthyoplankton assemblages at oceanic islands are still at the stage of describing general patterns (Boehlert et al., 1992; Leis, 1991), and those at seamounts are even less detailed. In this paper, we review the available information on 1) ichthyoplankton distributions at isolated seamounts and oceanic islands as they relate to spatial assemblages, 2) evidence that larvae of topographically associated species are maintained locally, and 3) the physical and biological mechanisms that may form, maintain, or disrupt assemblages near each type of topographic feature.

## SEAMOUNTS

*Physical Mechanisms.*—Local recruitment by retention of larvae above a seamount is an attractive hypothesis, but one not easily visualized in the face of diffusive and advective forces. Potential mechanisms retaining larvae must be characterized by specific time and space scales. The time scales most pertinent to the formation and maintenance of larval fish assemblages are on the order of weeks to months, involving spawning and egg and larval development. We consider two spatial scales pertinent to larval assemblages: the near-field area around small seamounts (<ca. 10 km summit diameter) and the far-field area surrounding seamount chains, very large banks, or seamount complexes.

Current-topography interactions on both scales at seamounts have received a great deal of attention from physical oceanographers. Perhaps most interesting is the generation of semi-stationary eddies (Taylor columns) above seamounts. Other oceanographic complexities are present at seamounts, however, including internal wave reflection (Eriksen, 1982), tidally induced currents and eddies (Meincke, 1971), trapped waves (Brink, 1989), and eddies shed downstream (Royer, 1978). To examine their potential role in maintenance of biological populations, one must consider the speed and temporal variability of impinging currents, the temporal stability of topographic effects, and the size and shape of the seamount of interest.

Taylor columns are characterized as closed-streamline anticyclonic vortices above topographic obstacles in an impinging flow (Fig. 1A). They have been predicted theoretically, demonstrated experimentally in the laboratory (Taylor, 1917; Huppert and Bryan, 1976), and observed in the field (Owens and Hogg, 1980; Dooley, 1984). They can extend from the seamount summit to the ocean surface or, in the case of a stratified ocean, to the bottom of the pycnocline (Bakun, 1988). Development of Taylor columns frequently involves upwelling along the seamount flanks (Bezrukov and Natarov, 1976). Shomura and Barkley (1980) first speculated that Taylor columns may maintain planktonic stages and facilitate recruitment, and suggested that differences in the biota and productivity among seamounts might be attributed to variability in the occurrence and intensity of Taylor columns. For small seamounts, the temporal persistence of trapped vortices is a key question. Development of a Taylor column is based upon seamount morphology, current speed, water column stratification, and the Coriolis parameter. At a given seamount, temporal variations in the impinging current flow (including tidal factors and other time-variant flows) and stratification are the causes of temporal variations in vortex development. Decreased current speeds can result in the breakdown of the vortex, whereas excessive speeds can result in eddies being shed downstream (Hogg, 1980). Under certain circumstances, tidal currents may generate similar vortices above seamounts; Meincke (1971) observed an anticyclonic vortex trapped above Meteor Seamount, and concluded that it was driven by tidal influences.

The persistence of Taylor columns relative to biological time scales is poorly known. Existing evidence at smaller seamounts does not support physical time scales that match the requisite biological time scales. Genin and Boehlert (1985) noted uplifted isotherms and higher chlorophyll levels over a small seamount and suggested the presence of a Taylor column with a likely residence time of a few days; it was not present 2 and 17 days later. Darnitsky et al. (1984) observed upwelling only twice over Wanganella Bank during six cruises in 4 years. Although longer periods of Taylor-column persistence (on the order of several months) were inferred from hydrographic and Eulerian current measurements above a deep

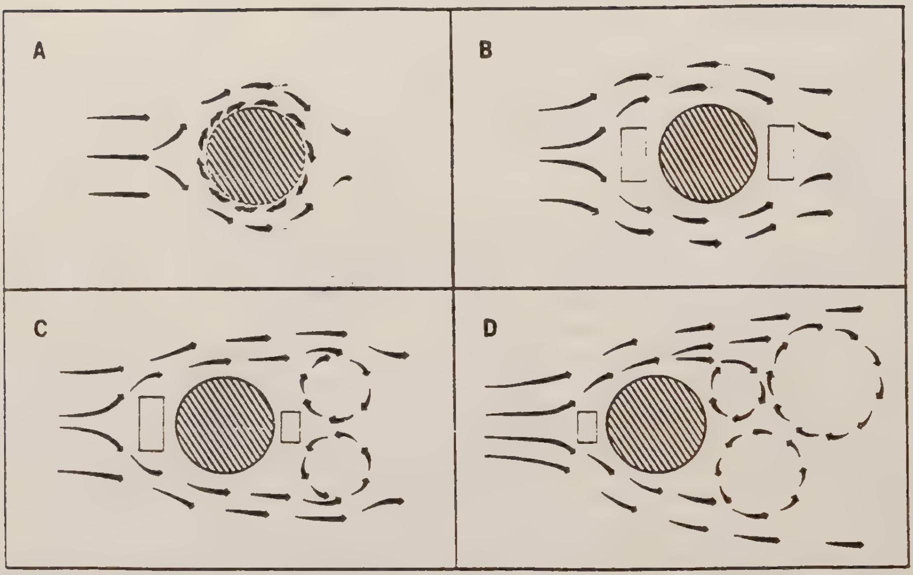

Figure 1. Variations in current-topography interactions. A. Interaction of flow with a seamount may lead to an eddy-like Taylor column remaining stationary over the summit (after Hogg, 1980). B–D. Interactions of a cylindrical island in a unidirectional current flow (after Hamner and Hauri, 1981). Slow current speeds result in laminar flow (B); increasing current leads to turbulent flow with downstream, contra-rotating eddies (C). Further increases lead to eddy shedding downstream (D). Stippled areas indicate stagnation points in the flow.

seamount in the North Atlantic (Owens and Hogg, 1980), the area was characterized by steady flow not commonly observed at shallow (<200 m) depths where most fish larvae occur.

At greater spatial scales (beyond the immediate area of the seamount summit), however, time scales may be appropriate for formation and maintenance of ichthyoplankton assemblages. Anticyclonic eddies shed from seamounts or seamount chains may remain in the general vicinity, as shown by Lagrangian current observations from satellite-tracked drifters (Cheney et al., 1980); retention of ichthyoplankton in the general region of seamounts may occur within such eddies for periods up to several weeks. These eddies can cause physical and biological variability in downstream waters (Royer, 1978; Genin et al., 1988), but detection of a biological signal (or larval fish assemblage) attributable to a seamount effect would require detailed biological and physical sampling as well as knowledge of the history of the water parcel.

At very large banks, some observations support the presence of quasi-stagnant water masses that may retain larvae. Eide (1979) observed this over a bank off the coast of Norway and found it consistent with the Taylor-column theory. Similar suggestions have been proposed for Rockall Bank, where Dooley (1984) noted episodic breakdowns of the gyral structure and suggested that these could have effects on variability in year-class strength of commercial fishes because of inconsistency in larval fish retention. Loder et al. (1988) characterized the oceanography at four large banks in the northwestern Atlantic, all of which have residual circulation indicative of anticyclonic motions around the bank. By considering the overall physical oceanography in light of time and space scales of water exchange in the around-bank, cross-bank, and vertical directions, they reduced highly complex flow patterns to more understandable terms relative to biological time and space scales. Of the four banks, only Georges Bank appeared to have water residence times approximately equal to or greater than the recirculation time of the gyre; it was thus the best candidate for consistent retention of larval stages and possibly assemblages.

*Seamount Ichthyoplankton.*—The first study of ichthyoplankton at a seamount was at the Great Meteor Seamount off North Africa in 1970 (Nellen, 1973, 1974). This seamount was not deemed to be conducive to the spawning and early survival of fishes but instead acted as a disturbance to the surrounding pelagic ecosystem. Larvae of oceanic species were reduced in numbers and diversity over the seamount summit. Nellen (1973, 1974) suggested that predation or physical damage during diel descent to the seamount plateau increased the mortality of vertically migrating oceanic species. In contrast, larvae of two topographically associated species were more abundant at the summit than in the surrounding ocean. From this, he suggested that non-migrating larvae of species spawning over the seamount were maintained by currents. Larvae of euneustonic species were neither more abundant nor subject to increased mortality at the seamount. Nellen (1973) suggested two influential hypotheses: hydrography may maintain larvae of species spawning over seamount summits; and predation and exclusion of migrators reduce the abundance of oceanic larvae over seamounts.

These hypotheses are neither entirely supported nor refuted by other studies. Later sampling at the Great Meteor Seamount failed to find concentrations of topographically associated species (Belyanina, 1984). No evidence of retention of larvae was found at seamounts in the Indian Ocean (Belyanina, 1985). Conflicting results were obtained from samples taken within and between seasons at a seamount in the central North Pacific Ocean (Boehlert and Genin, 1987; Boehlert, 1988). In summer, larval fish densities were not different above and away from the summit during the day in three of the four depth strata sampled, but were more abundant away from the summit at all depths at night. In winter, larvae were more abundant over the summit than away from it at all depths during day and night (Boehlert and Genin, 1987). Boehlert (1988) suggested an interaction of three factors to explain the biological observations: first, semi-stationary eddies could maintain larval fish populations over the summit; second, vertically migrating taxa would be excluded from the summit's region by its physical presence; and third, predation at the summit would reduce the abundance of oceanic taxa. He concluded that none of the factors alone could explain the observations, but their interaction probably increased biological variability in the ocean above and downstream from the seamount.

There have been no studies explicitly identifying ichthyoplankton assemblages at seamounts. Three generalities about groups of fish larvae found at seamounts may be extracted from published studies: 1) the dominant larvae at most seamounts are widespread oceanic species (typically oceanic species of the Myctophidae and the Stomiiformes); 2) larvae of topographically associated species are rare at all but shallow seamounts; and 3) the abundance of larvae of topographically associated species often decreases with increasing distance of seamounts from larger land masses.

Surprisingly few studies have found larvae of topographically associated species to be more abundant at seamounts than in the surrounding ocean. Larvae of benthic species were found to be dominant in only one study (Robertson and Mito, 1979), a gadiform, *Gaidropsarus novaezealandiae*, and a bovichtid, *Bovich-*

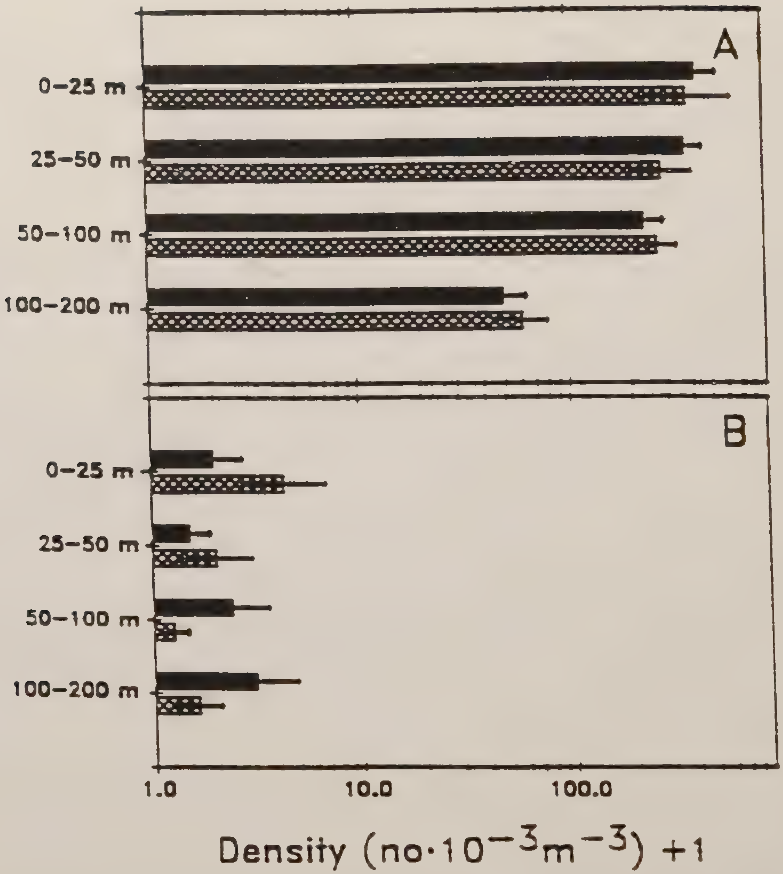

Figure 2. Densities of oceanic larvae (A) and seamount-associated (demersal or benthopelagic) larvae (B) at Southeast Hancock Seamount in July 1984 (summer) and February 1985 (winter) with replicate samples during day and night at four discrete depths (from Boehlert and Mundy, unpubl.). Solid bars indicate densities over the seamount summit; cross-hatched bars indicate densities at a station 20 km west of the summit. Error bars indicate ±1 SE.

*tus variegatus*, at banks off New Zealand. Larvae of seamount-associated species were notably rare in studies at the Hancock Seamount in the central North Pacific Ocean (Boehlert, 1988). On average, they were at least one hundred times less abundant than oceanic species (Fig. 2). The rarity of larvae of topographically associated species at this seamount is unexpected, because it supports large populations of demersal fishes (Sasaki, 1986).

Detailed examination of the distribution of larvae at Southeast Hancock Seamount provides further evidence that larvae of most species were not retained over the seamount summit. Sampling consisted of two cruises (July 1984 and February 1985) with stations above and 20 km to the west of the seamount summit in each cruise; samples at both stations were taken in four discrete depth strata (Boehlert and Genin, 1987; Boehlert, 1988; Fig. 2). Additional samples were taken in the neuston (0 to 1 m) in winter. Seamount taxa at 0 to 50 m were most abundant away from the seamount (Fig. 2). The dominant species in these strata was *Beryx splendens*, collected only in summer (Mundy, 1990). Only in the two deepest strata (50 to 200 m) were larvae of seamount taxa more abundant over the seamount summit than away from it (Fig. 2). These were almost all *Maurolicus muelleri*, which were collected only in winter (Boehlert and Mundy, unpubl.). Larvae and small juveniles of *Pseudopentaceros wheeleri*, the dominant species in samples of adult fishes at this seamount, were only collected in neuston tows. Dispersal of *P. wheeleri* away from seamounts may actually be enhanced by the exclusive occurrence of their larvae in the neuston (Boehlert and Sasaki, 1988), where wind-driven advection will rapidly disperse the larvae away from their source. Thus, evidence exists for greater abundance of larvae of only one species, *M. muelleri*, over Southeast Hancock Seamount. Demonstrating retention of larvae at the seamount, however, will require more detailed information on ocean currents and the distribution of late larval stages.

The frequency of occurrence and abundance of larvae of topographically associated species decrease with increasing distance of seamounts from larger land masses and increasing summit depth. Nellen (1973, 1974) suggested that although the neritic species with abundant larvae were spawning at the Great Meteor Seamount, reproduction there was unlikely to sustain populations. Such "dependent populations" have also been noted at seamounts in the central North Pacific (Belyayev, 1990). In the Indian Ocean, larvae of shallow water fishes were absent from two seamounts isolated from continental areas and present at two seamounts closer to shelf areas (Belyanina, 1985). A similar pattern was found in a more intensive study of one deep (182 m) and three shallow (10 m) seamounts in the same region (Gordina and Bladimirtsev, 1987). In the latter study, larvae of neritic species were most abundant at shallow seamounts.

Several sampling problems are apparent with existing surveys of ichthyoplankton around small seamounts. First, temporal sampling patterns have been inadequate to detect seasonal peaks of larval abundance for certain species. Second, spatial sampling in the studies identified above is typically restricted to stations above the summit and at some distance away from the summit. Thus, analysis of the spatial distributions of larvae was often based upon paired comparisons, as opposed to a broader geographic analysis and consideration of variables such as current direction. A related problem is that almost no studies have reported measurements of currents simultaneous with ichthyoplankton collections. Gordina and Bladimirtsev (1987) found that larvae of neritic species were concentrated in eddies downstream of shallow (10 m) seamounts, rather than directly above the summit centers. Oceanic larvae dominated in upstream areas. The distribution of neritic larvae was given as evidence that such larvae may be advected from their source but retained in the vicinity of shallow seamounts by eddies.

The problems of spatial sampling and oceanographic measurements have been better addressed at certain large banks. Rockall Bank (Dooley, 1984), Georges Bank (Smith and Morse, 1985), and Browns Bank (Campana et al., 1989) show characteristic eddies that have been proposed to maintain eggs and larvae through the planktonic stages to promote local recruitment. Even so, Campana et al. (1989) suggested, the Browns Bank mechanism was a "leaky gyre," and cohorts of larval haddock, *Melanogrammus aeglefinis*, were split into retained and vagrant groups. Above some threshold size, banks may have self-sustaining populations, but typically with species characteristic of adjacent continental shelves or slopes. The processes described in Loder et al. (1988) seem to be applicable in such cases.

To summarize, seamount ichthyoplankton assemblages containing topographically associated species have been most frequently identified near shallow (<200

m) summits which are near larger land masses. There is little evidence that persistent ichthyoplankton assemblages, distinct from those in the surrounding ocean, exist near deeper, more isolated seamounts. The physical interference of seamounts with vertical migration and the high predation rates at seamount flanks and summits generally act to increase variability in plankton at seamounts and downstream therefrom (Genin et al., 1988). Thus, fish that spawn at seamounts may be subject to extreme variability in recruitment due to dispersal of larvae away from adult habitats. Recruitment to seamounts may depend more upon occasional events than it does at oceanic islands. Recruitment of many species at seamounts may also include major input from populations at larger land masses (Nellen, 1973; Vasilenko and Sokolovskaya, 1989). The combination of highly variable and occasionally allochthonous recruitment may help explain several features of fish populations at seamounts, including the lower than expected rate of endemism (Wilson and Kaufman, 1987), susceptibility of seamount populations to recruitment overfishing (Sasaki, 1986), and unpredictable recovery after overfishing (Lutjeharms and Heydorn, 1981).

## OCEANIC ISLANDS

An early hypothesis about the distribution of larval fishes at oceanic islands suggested that larval Acanthuridae might be retained in their vicinity by small eddy systems (Randall, 1961). Sale (1970) found larval acanthurids to be more abundant offshore (48 to 58 km) than near Oahu, Hawaii (4.8 to 8.0 km), and also proposed that eddies returned these larvae to the island. These suggestions have been generalized to other families of fishes (Johannes, 1978). Prior to the publications of Miller (1974) and Watson and Leis (1974), however, there was almost no empirical information on the distribution of ichthyoplankton near oceanic islands to allow informed speculation about these ideas.

Early surveys off Oahu suggested that fish larvae were not distributed near islands as if they had passively diffused from the island source (Miller, 1974). Distinct differences in the distributions of taxa indicated the influence of behavioral differences (Watson and Leis, 1974). Larvae of certain highly visible reef families, including the Acanthuridae, Chaetodontidae, Labridae, and Scaridae, were rare in nearshore samples (Miller, 1974; Leis, 1978). The early suggestion that some types of larvae occur far from shore (Sale, 1970) has been verified. Larvae of labrids and pomacentrids, for example, have been found 370 to 1200 km from the nearest adult habitat (Leis, 1983; Victor, 1987). The occasional occurrence of such larvae at extreme distances does not mean that they are most abundant away from land; several taxa often considered to have widely dispersed larvae are actually most abundant at intermediate distances from shore (Wyatt, 1982; Young et al., 1986; Leis, 1989; Clarke, 1991).

The planktonic habitat near oceanic islands is occupied preferentially not only by larvae of topographically associated fishes, but also by larvae of certain oceanic fishes (Miller, 1979; Leis et al., 1991). The importance of this habitat to these oceanic species is unknown. As an example, the increased nearshore abundance of tuna larvae in the genus *Thunnus* (Fig. 3) may simply be a result of the higher abundance of spawning adults near islands. Tunas typically aggregate near islands and banks for feeding (Uda and Ishino, 1958), but larvae are not regularly concentrated in other areas of adult occurrence, such as fronts. An alternate hypothesis is that waters around islands are more suitable for survival of early larvae, perhaps through improved feeding conditions. Primary productivity around islands, may be higher than in the open ocean (the "island mass" effect), particularly around

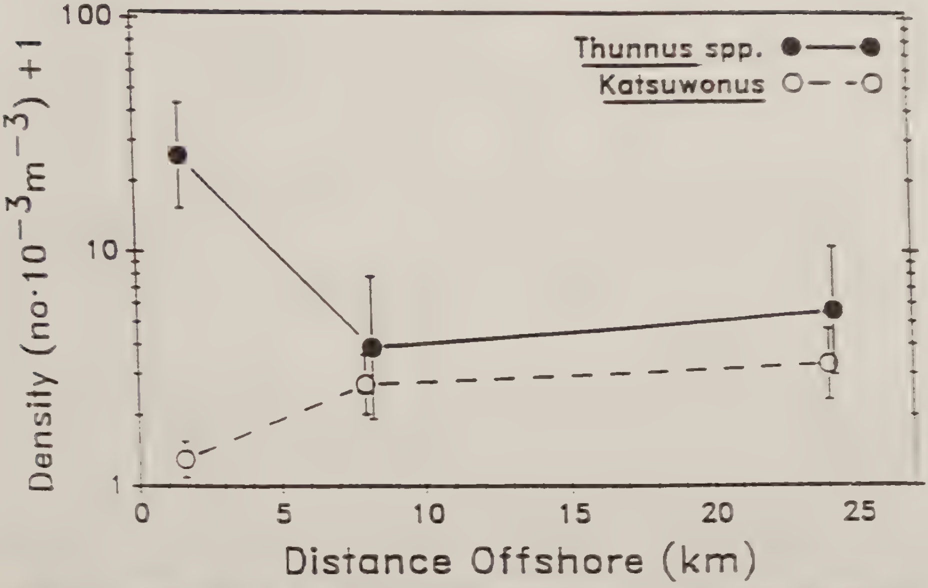

Figure 3. Onshore-offshore patterns of distribution of *Thunnus* spp. and *Katsuwonus pelamis* collected during June 1986 off the leeward coast of Oahu, Hawaii. Values are means from discrete-depth samples taken in the upper 40 m for *Thunnus* spp. (N = 10 nearshore station, N = 6 at each offshore station) and the upper 80 m for *K. pelamis* (N = 16 nearshore station, N = 10 at each offshore station). Error bars indicate ±1 SE.

high islands, such as Oahu (Gilmartin and Revelante, 1974; Dandonneau and Charpy, 1985). Waters near islands in tropical and subtropical areas may also be characterized by increased zooplankton abundance, often of species uncommon in offshore waters (Jones, 1962; Hernandez-Leon, 1988, 1991). Thus, greater availability of prey in nearshore waters could result in higher survival rates for early larvae during the stage when prey density requirements are highest (Hunter and Kimbrell, 1980). In the case of *Thunnus* spp., Higgins (1970) noted a threefold higher abundance of juveniles at stations 56 km, as opposed to 7 km, offshore of Oahu. Such oceanic larvae may thus disperse from nearshore areas with increasing age as their prey-searching capabilities improve. The case is made, however, for possible enhanced survival for larvae developing in waters around islands.

*Sampling Problems.*—Description of the distributions of larvae of many island-associated fishes has been hampered by their low abundance in the plankton. Larvae of one of the most visible coral reef families, the Chaetodontidae, comprise <0.5% of the total larvae in ichthyoplankton surveys (Leis, 1989). Clarke (1991) noted that the average densities of many taxa 13 km off Oahu, including those previously described as rare inshore, typically range from 0.0001 to 0.01·1,000 $m^{-3}$. He pointed out that it is necessary to sample water volumes >1,000 $m^3$ to describe the distributions of most island-associated species. This has not been done in most studies. The sampling problems of accurately describing the distributions of naturally sparse fish larvae enhance the utility of examining larval fish assemblages. Patterns may be detected in assemblages that are obscured by the patchy distribution or low sample sizes of individual taxa.

Spatial and temporal scales of sampling have often been insufficient to identify the spatial extent or temporal persistence of assemblages. The time and space scales pertinent to larval fish assemblages around islands vary with island size but are ill-defined for virtually all islands. The biological time scales are on the order of weeks to months, the characteristic time scale for the pelagic period prior to recruitment to the juvenile or adult habitat (Thresher and Brothers, 1989). Spatial scales of biological interest are dependent upon the habitat type used by the species of fish (demersal or pelagic), the spawning type (pelagic or demersal egg), and perhaps the distances characterizing diffusive and advective processes over the relevant time scale. Most studies of island ichthyoplankton have conducted onshore-offshore transects to analyze patterns of larval fish distribution. Because spatial sampling has largely ignored the larger scale of distribution around islands, spatial variation in assemblage distribution is poorly known. Thus, discussion of physical mechanisms relative to larval fish distribution around islands has been largely speculative.

*Early Evidence for Assemblages in Island Systems.*—The first suggestions that different assemblages of larvae exist at oceanic islands came from studies off Oahu. Miller (1974) noted that fish larvae were more concentrated in nearshore (<10 m depth) than offshore (>10 m depth) areas, larvae of certain offshore species were abundant inshore, and the abundance of larvae from demersal eggs was inversely correlated with the abundance of larvae of mesopelagic species. Watson and Leis (1974) found that larvae of pelagic bay species with pelagic eggs and reef species with demersal eggs were abundant within an embayment on Oahu. Larvae of oceanic species and reef species with pelagic eggs were rare in the bay; Watson and Leis (1974) suggested that these larvae completed their planktonic life in offshore waters. From this series of studies, Leis and Miller (1976) concluded that larvae of insular species from demersal eggs occur more frequently in a nearshore assemblage, while those from pelagic eggs are more frequent offshore.

The assemblages identified at Oahu form the basis for almost all subsequent work around islands. Evidence for at least four larval fish assemblages can be found in studies of ichthyoplankton distributions around islands subsequent to Leis and Miller's (1976) work: 1) assemblages unique to embayments and lagoons, 2) extreme nearshore assemblages, 3) intermediate nearshore assemblages, and 4) offshore assemblages. The latter three will be referred to as the "nearshore," "neritic," and "oceanic" assemblages, following Leis (1978).

*Embayment Assemblages.*—The presence of distinct assemblages in embayments and lagoons of oceanic islands (referred to as "embayment assemblages," for brevity) has not been investigated in detail. Although Leis (1981) did not observe a nursery function in a small reef lagoon within the Great Barrier Reef, larger lagoons and embayments on certain oceanic islands may differ in this respect. Preliminary results of studies at oceanic atolls in the Coral Sea (Leis, 1986a) and at French Polynesia (Leis, 1991) suggest that larval fish assemblages there consist of species not found in abundance outside of lagoons. The Gobiidae, Apogonidae, Pomacentridae, and Blenniidae are the dominant families in these assemblages. The initial suggestion that an embayment at Oahu had a unique assemblage of larvae (Watson and Leis, 1974) was corroborated by Leis and Miller (1976), Miller et al. (1979), and Kobayashi (1989; Table 2).

Recent collections within the lagoon of Palmyra Atoll, Line Islands, contained mostly larvae that were not found in samples outside of the reef, including many samples taken within 0.5 km of the atoll (Boehlert and Mundy, unpubl.). These lagoonal collections were also composed almost entirely of larval Gobiidae, Apogonidae, Pomacentridae, and Blenniidae. Thus, larval fish assemblages in enclosed

Table 2. Selected taxa included in larval fish assemblages proposed in studies at tropical and subtropical islands. The assemblages are those found in embayments (estuaries, lagoons, and other semi-enclosed areas), nearshore waters (0 to 0.5 km offshore), neritic waters (0.5 to 3–5 km offshore), and oceanic waters (3–5 to 600 km offshore). Egg types are noted because some assemblages were suggested to be dominated by larvae from either pelagic or demersal (including brooded or viviparous) eggs. Ubiquitous pelagic species are excluded because they form the background field of larvae to which island taxa are added

| Taxon | Assemblage | Reference | Egg type |
|---|---|---|---|
| Engraulididae | neritic | 12 | pelagic |
| *Encrasicholina purpurea* | embayment | 6, 13 | pelagic |
| *E. punctifer* | neritic? | 7 | pelagic |
| | oceanic | 2, 5 | pelagic |
| Clupeidae | | | |
| *Jenkinsia* sp. | nearshore | 17, 20 | unknown |
| *Spratelloides delicatulus* | nearshore | 7 | demersal? |
| Myctophidae | | | |
| *Benthosema fibulatum* | neritic | 1 | pelagic |
| *Lampadena urophaos* | nearshore | 7 | pelagic |
| | neritic | 1, 7 | pelagic |
| Synodontidae | nearshore | 20 | pelagic |
| | neritic | 3 | pelagic |
| | oceanic | 4 | pelagic |
| Ophidiidae | nearshore | 20 | pelagic? |
| Bythitidae | nearshore | 2 | livebearer |
| Exocoetidae | neritic | 13 | pelagic |
| Holocentridae | neritic? | 4 | pelagic |
| Pegasidae | oceanic | 5 | unknown |
| Syngnathidae | nearshore | 20 | brooded |
| Scorpaenidae | neritic | 12 | pelagic |
| Symphysanodontidae | oceanic | 4 | pelagic |
| Serranidae | oceanic | 4, 13 | pelagic |
| Apogonidae | embayment | 2, 6, 10, 13 | brooded |
| | nearshore | 12 | brooded |
| | neritic | 12, 13 | brooded |
| | oceanic | 13 | brooded |
| Epigonidae | neritic | 3, 7 | pelagic |
| | oceanic | 3 | pelagic |
| Lutjanidae | neritic? | 4 | pelagic |
| Mullidae | nearshore | 10, 12 | pelagic |
| | neritic | 13 | pelagic |
| Haemulidae | nearshore | 20 | pelagic |
| Pempherididae | nearshore | 20 | pelagic |
| Sciaenidae | | | |
| *Pareques iwamotoi* | nearshore | 18 | pelagic |
| Chaetodontidae | oceanic | 3, 7, 11, 15 | pelagic |
| | neritic | 3, 11 | pelagic |
| Pomacanthidae | oceanic | 4 | pelagic |
| Carangidae | embayment | 13 | pelagic |
| | neritic | 13 | pelagic |
| | oceanic | 4 | pelagic |
| *Gnathanodon speciosus* | embayment | 2 | pelagic |
| Pomacentridae | embayment | 13 | demersal |
| | nearshore | 7, 10, 12 | demersal |
| | neritic | 12, 13 | demersal |
| | oceanic | 13 | demersal |
| *Abudefduf abdominalis* | neritic | 7, 8 | demersal |
| *Stegastes* sp. | oceanic | 21 | demersal |
| Labridae | neritic | 3, 12 | pelagic |
| | oceanic | 4, 7, 13, 15, 21 | pelagic |
| *Thalassoma* sp. | oceanic | 9, 21 | pelagic |

Table 2. Continued

| Taxon | Assemblage | Reference | Egg type |
|---|---|---|---|
| Scaridae | neritic | 3 | pelagic |
| | oceanic | 3, 7, 15 | pelagic |
| Gobiesocidae | nearshore | 2, 20 | demersal |
| Callionymidae | neritic | 12 | pelagic |
| | oceanic | 4 | pelagic |
| Pinguipedidae | neritic | 3 | pelagic |
| | oceanic | 4 | pelagic |
| Creediidae | neritic | 3 | pelagic |
| Blenniidae | embayment | 10, 13 | demersal |
| | nearshore | 7, 12 | demersal |
| | neritic | 3, 13 | demersal |
| | oceanic | 13 | demersal |
| *Exallias brevis* | neritic | 7, 8 | demersal |
| Tripterygiidae | nearshore | 2, 7, 8, 10, 12 | demersal |
| Gobioidei | embayment | 6, 13 | demersal |
| | nearshore | 2, 7 | demersal |
| | neritic | 7, 8, 12, 13 | demersal |
| | oceanic | 4 | demersal |
| *Amblygobius* sp., others | embayment | 2 | demersal |
| *Eviota epiphanes* | neritic | 1, 3, 7, 8 | demersal |
| Schindleriidae (larvae and adults) | | | |
| *Schindleria pietschmanni* | nearshore | 7 | demersal? |
| | neritic | 3 | demersal? |
| *Schindleria praematura* | embayment | 2 | demersal? |
| | neritic | 7, 8 | demersal? |
| Acanthuridae | oceanic | 4, 7, 13, 15, 19 | pelagic |
| Scombridae | neritic | 13, 14 | pelagic |
| *Thunnus albacares* | nearshore | 7 | pelagic |
| | neritic | 1, 16 | pelagic |
| Bothidae | neritic | 3 | pelagic |
| | oceanic | 13 | pelagic |
| Molidae | neritic | 13 | pelagic |
| | oceanic | 13 | pelagic |

1. Boehlert and Mundy (unpubl. data, Oahu); 2. Boehlert and Mundy (unpubl. data, Palmyra Atoll); 3. Boehlert et al. (1992); 4. Clarke (1991); 5. Hirota et al. (1980); 6. Kobayashi (1989); 7. Leis (1978); 8. Leis (1982); 9. Leis (1983); 10. Leis (1986b); 11. Leis (1989); 12. Leis and Goldman (1987); 13. Leis and Miller (1976); 14. Leis et al. (1991); 15. Miller (1974); 16. Miller (1979); 17. Powles (1977); 18. Powles and Burgess (1978); 19. Sale (1970); 20. Smith et al. (1987); 21. Victor (1987)

waters of oceanic islands may be qualitatively very different from those in enclosed lagoons of continental islands and tropical coasts (Table 2).

*Nearshore Assemblages.*—There is increasing evidence that some fish species have larvae found primarily at distances of 0 to 500 m from substrates (Barnett et al., 1984; Powles et al., 1984; Marliave, 1986; Jahn and Lavenberg, 1986). Leis (1978) described the assemblage at 200 m off leeward Oahu (Table 2). In a discussion of fish larvae at the Great Barrier Reef, which is not an island environment, Leis (1986a) noted that tripterygiids were among a special assemblage of larvae that could be frequently found ". . . in waters immediately to windward of coral reefs . . ." but which were ". . . found in high numbers nowhere else." This pattern was also found in a study at Palmyra Atoll, where the dominant larvae in samples collected <500 m from shore were tripterygiids, bythitids, gobiesocids, and certain gobiids, with this assemblage particularly abundant in a restricted portion of the island's circumference (Boehlert and Mundy, unpubl.). A comparison of larval densities north and south of the island in samples taken along the 100-m isobath, for example, shows dramatic differences (Fig. 4), with the greatest abundance on

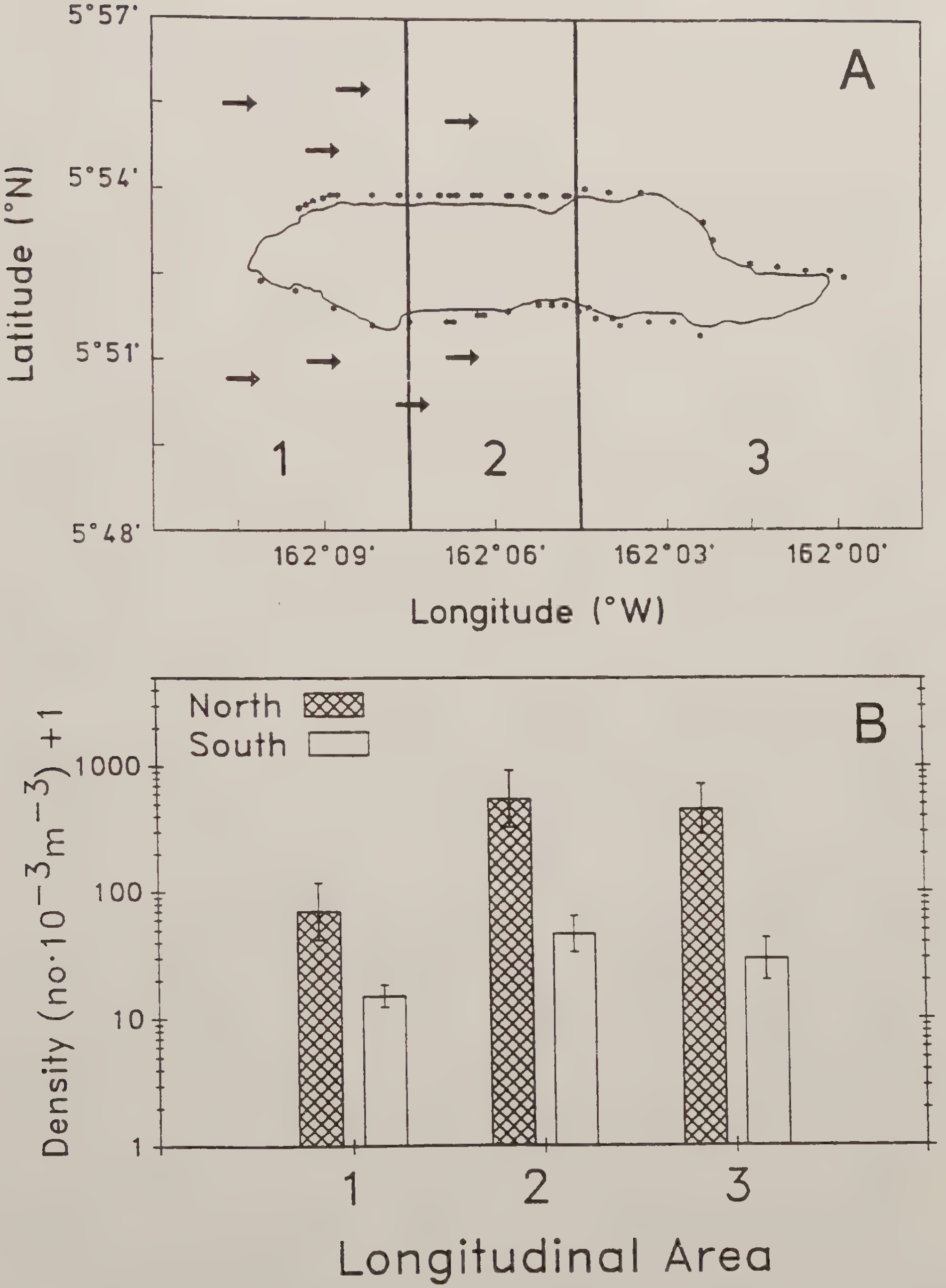

Figure 4. Larval fish distributions surrounding Palmyra Atoll in the central equatorial Pacific (Boehlert and Mundy, unpubl.). A. Outline of the 10-m isobath surrounding the island, with the sampling stations indicated by asterisks. All samples were taken during daylight hours with a 1-m² MOCNESS in the upper 50 m. Data are divided into three longitudinal strata. General current direction is indicated by arrows. B. Mean larval fish densities by longitudinal stratum, divided to north and south sides of the island.

the northern side of the island. Thus, although the taxonomic composition of nearshore assemblages varies between studies, there is increasing evidence that such assemblages predictably occur near islands.

Within the nearshore assemblage, other types of larvae may have even more restricted distributions (Table 2). Larvae of the clupeid genus *Jenkinsia* (Powles, 1977) and of the sciaenid *Pareques iwamotoi* (Powles and Burgess, 1978; Miller and Woods, 1988) were found extremely close to the bottom (<2 m) near coral heads. In the Virgin Islands, Caribbean Sea, larvae that were rare in towed net samples were taken near reefs and at the lights of an undersea habitat (Smith et al., 1987). In Kaneohe Bay, Oahu, Hawaii, larvae of two gobiid species also were found to be most abundant within a few meters of coral reef heads (Kobayashi, 1989). These may be tropical, insular examples of larvae that are restricted in distribution to within a few meters of a substrate (Marliave, 1986). This near bottom habitat is sorely undersampled in island waters, as elsewhere.

*Neritic Assemblage.* —Most studies of larval fish distributions around islands have found evidence for an assemblage of larvae distributed in a band of approximately 0.5 to about 3 to 5 km from shore, but these distances may vary around different parts of islands, depending upon current strength and island morphology. The neritic assemblage is typically dominated by insular taxa with demersal eggs and a few oceanic taxa (Table 2). The contribution of insular taxa with planktonic eggs to this assemblage is not yet resolved, with more investigation being clearly required (Clarke, 1991). Components of the neritic assemblage off leeward Oahu vary between studies because of different analysis techniques. Leis (1978, 1982) identified an assemblage from an analysis of absolute abundances, while Leis and Miller (1976) used relative densities of larvae. Miller et al. (1979) combined the nearshore and neritic assemblages in their analysis.

A neritic assemblage similar to that off Oahu was found close to the lee of Johnston Island, an isolated atoll several hundred kilometers southwest of Hawaii (Boehlert et al., 1992). That study sampled a grid around the island on a scale pertinent to the neritic assemblage. An assemblage consisting of three groups of strictly island-related species was noted (Table 3). Two of the groups were small, with two and three taxa that were fairly rare but most abundant in the 50- to 100-m depth stratum. The largest group was composed of highly abundant taxa present in areas beyond the neritic area and throughout the upper 200 m but clearly most abundant in neritic waters in the 50- to 100-m stratum (Boehlert et al., 1992). The scale of the areas of high abundance for this assemblage relative to the island, however, was markedly greater than the distances normally seen in neritic assemblages and encompassed distances of ≤10 km downstream of the island, whereas the assemblage was rare upstream of the island, as would be expected (Fig. 5A). Similar upstream/downstream differences in larval fish abundance were noted at this scale at Jamaica (Wyatt, 1982).

The oceanic species found in neritic larval fish assemblages include three components: species associated with topography as adults, within families usually considered mesopelagic; widely distributed species with larvae abundant in all regions; and those with larvae concentrated in neritic regions. Examples of topographically associated species with larvae found in the neritic assemblage include *Lampadena urophaos* (Leis, 1978) and *Benthosema fibulatum* (Boehlert and Mundy, unpubl.) off Oahu, and *Scopelosaurus gibbsi* off Muraroa (Bourret et al., 1979). Widely distributed species with widely distributed larvae include *Ceratoscopelus warmingi* (Leis, 1978). A group of ubiquitous larvae that acted as a background field contributing to neritic and oceanic assemblages at Johnston Atoll included nine species that were present in over 66% of all samples (Table 3).

Table 3. Larval assemblages identified from an ichthyoplankton survey surrounding Johnston Island in the central tropical Pacific Ocean. Depths sampled included 0–50 m, 50–100 m, and 100–200 m. The species groups within assemblages were determined with a two-way synthesis table technique. Several other abundant species were not characterized by distributions coherent with other groups (from Boehlert et al., 1992)

| |
|---|
| Neritic Larval Assemblage |
| *Eviota epiphanes*, Salariini, *Limnichthys donaldsoni*, *Parapercis* sp., *Schindleria pietschmanni*, Labridae (present in nearly all depths and habitats, but most abundant in neritic area at 50–100 m) |
| *Selar crumenophthalmus*, Tetraodontidae, *Apogonichthys perdix* (greatest abundance in neritic area at 50–100 m) |
| *Synodus* spp., Bothidae (greatest abundance in neritic area at 50–100 m depth) |
| Mixed Neritic and Oceanic Larval Assemblage |
| *Epigonus* sp., Scaridae, Chaetodontidae, *Nealotus tripes* (greatest abundance in neritic and offshore areas, 0–50 m depth strata) |
| Oceanic Larval Assemblage |
| *Lestidium* spp., *Diaphus pacificus*, *Sudis atrox*, *Evermannella* sp. (present in nearly all depths and habitats, but greatest abundance in 50–200 m, both neritic and offshore areas) |
| *Coryphaena hippurus*, *Cubiceps caeruleus*, *Bathophilis* sp., *Caulophyrne* sp. (greatest abundance in offshore area, 0–50 m depth stratum) |
| *Melamphaes* spp., *Bregmaceros* sp., *Howella* sp., *Hygophum reinhardti* (greatest abundance in offshore area, 50–200 m depth) |
| *Idiacanthus* sp., *Gonostoma atlanticum*, *Gonostoma* spp. (present neritic and oceanic areas, most abundant at 100–200 m) |
| *Scopelosaurus* spp., *Gonostoma elongatum*, *Scopelarchus* spp. (present oceanic areas, most abundant at 100–200 m) |
| Ubiquitous Larval Taxa |
| *Ceratoscopelus warmingi*, *Vinciguerria nimbaria*, *Diaphus* spp., *Cyclothone* spp., *Lampanyctus nobilis*, *Bolinichthys* spp., *Symbolophorus evermanni*, *Hygophum proximum*, *Lampadena urophaos* |
| (present in more than two-thirds of all samples in the study, not included in the analytic procedure for defining assemblages) |

These were not included in the assemblage analysis by Boehlert et al. (1992). Three of five assemblages of rarer oceanic taxa were less abundant in the neritic region, suggesting the possibility of exclusion from neritic waters, whereas two others were ubiquitous across areas. Examples of widely distributed taxa with larvae concentrated in neritic areas include *Thunnus albacares* (Fig. 3; Miller, 1979; Leis et al., 1991; Boehlert and Mundy, 1991) and the Istiophoridae (Leis et al., 1987).

*Oceanic Assemblage.*—The inshore limit of the oceanic assemblage around islands is found 2 to 5 km offshore; the seaward limit of this assemblage is poorly known (Leis and Miller, 1976). Note that "oceanic" in this context does not refer to an assemblage consisting only of larvae of oceanic species; rather, it refers to the assemblage containing larvae of insular taxa found at the greatest distance from an island in oceanic waters (Table 2).

The inshore distance for the transition between oceanic and neritic assemblages is most probably an artifact of sampling effort; identification of the true distance and its variability will depend upon continuous sampling in offshore transects covering different regions of an island. The offshore extent of oceanic assemblages is unknown largely because of limited sampling. Larvae of island-associated taxa have been found at great distances from the nearest adult habitat (Leis, 1983;

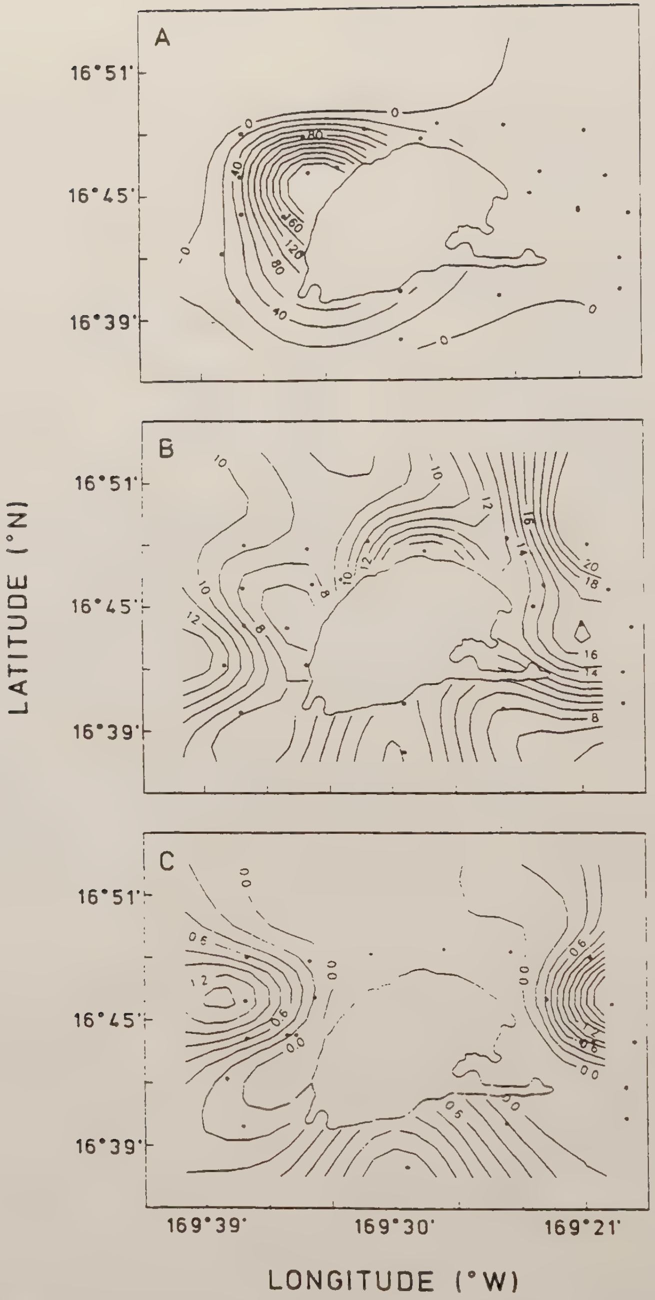

Figure 5. Distribution of ichthyoplankton around Johnston Island: the outline surrounding the island represents the 18-m isobath (data from Boehlert et al., 1992). General current flow in the region is from east to west with a moderately stagnant area downstream of the island where the highest densities in 5A occur. All density notations are in larvae per 1,000 m$^3$. 5A. Distribution of the combined densities of species included in the first neritic assemblage (Table 3: assemblage A, dominated by *Eviota epiphanes*) in the 50 to 100 m depth stratum. 5B. Distribution of the second oceanic assemblage (Table 3: oceanic assemblage B, with *Coryphaena hippurus*) in the 0 to 50 m depth stratum. 5C. Distribution of the ubiquitous mesopelagic species *Vinciguerria nimbaria* in the 50 to 100 m depth stratum.

Victor, 1987), but are probably not frequent or abundant components of larval fish assemblages at these distances (Leis, 1984; Clarke, 1991). Regional differences may exist, however, and the presence of island-associated taxa extends to a radius of 100 to 300 km from islands in the Pacific Ocean and 300 to 600 km in the Indian Ocean (Fedoryako, 1989). Aoki and Ueyanagi (1989) suggested that *Coryphaena hippurus* occurred in association with oceanic islands, whereas its congener *C. equiselis* was distributed throughout oceanic waters. *Coryphaena hippurus* was included in one of the groups within the oceanic assemblage around Johnston Island (Table 3; Boehlert et al., 1992). The distribution of this assemblage around the island, however, was regionally variable (Fig. 5B); it occurred in very low densities near the island and increased in density with distance offshore. *Vinciguerria nimbaria*, a species ubiquitous in distribution, also had lower densities near the island than offshore (Fig. 5C). This species and the oceanic assemblage (Fig. 5B) were least abundant in the area where the dominant neritic assemblage was found in highest abundance (Fig. 5A). This suggests that maintenance of locally spawned species occurred, as opposed to concentration of all species. The role of behavior in maintaining this distribution pattern is unknown.

Following Leis and Miller (1976), most studies have included larvae of insular species with planktonic eggs in oceanic assemblages, along with the widely distributed, truly oceanic species (Leis 1978, 1982; Miller et al., 1979). Similar results can be found in studies of larvae from Australia, a continental rather than insular system (Young et al., 1986; Leis and Goldman, 1987). It is interesting to note, however, that the only assemblage at Johnston Island with a mix of oceanic and island-related taxa included the Chaetodontidae and Scaridae, with a distribution pattern showing abundance in both neritic and oceanic waters (Table 3). Investigations are thus demonstrating that not all families, or even all taxa within families with pelagic eggs, are as widely dispersed in oceanic assemblages as previously thought (Leis, 1987, 1989; Boehlert et al., 1992). Resolution of these patterns will require more investigation with techniques that overcome the sampling problems noted by Clarke (1991).

*Physical and Behavioral Mechanisms.*—That islands, particularly in tropical regions, are areas of relatively high productivity seems to be related to vertical mixing and upwelling associated with current-topography interactions (Heywood et al., 1990). These interactions are different from those around seamounts and will not be reviewed in detail here. Instead, the focus is how these interactions relate to the formation, maintenance, and breakdown of larval fish assemblages. [For a more comprehensive background on island-current effects, see reviews in Hogg (1980), Hamner and Hauri (1981), and Wolanski and Hamner (1988).]

Formation and maintenance of embayment assemblages probably depend upon a combination of boundary-layer effects, longer retention times for water, and behavior of larvae. Retention of larvae may be proportional to flushing times (Sammarco and Andrews, 1989), and larger, deeper lagoons typically have longer flushing times; moreover, wind-driven, two-layered circulation patterns exist in atoll lagoons (Atkinson et al., 1981). It is thus possible that larvae can behaviorally alter horizontal distribution with vertical movements (Doherty et al., 1985). Boundary mixing in coral reef lagoons is responsible for virtually all of the vertical mixing (Wolanski, 1987), but there is some evidence that the magnitude of mixing is sufficiently low in embayments and lagoons to allow larvae to maintain position. Kobayashi (1989), for example, observed consistent patterns of larval fish distributions at differing distances from patch reefs, suggesting visually mediated behavior in this fine-scale distribution. Epibenthic behavior of postflexion larvae has been suggested to maintain larvae in specific areas (Leis et al., 1989; Breitburg, 1989); this presumably involves visual behavior and orientation to both the bottom and, in the case of schooling, to other individuals.

Physical mechanisms important for nearshore assemblages are similar but probably more varied. Localized benthic boundary layers may exist in certain areas with reduced flow, allowing aggregations of larvae (Hamner and Hauri, 1981). In contrast, highly turbulent mixing in surf zones would preclude position maintenance by larvae (Bakun, 1988). The larval fishes that have been observed in surf zones are typically later-stage larvae over relatively smooth bottoms (Senta and Kinoshita, 1985). Larger-scale interactions of currents and islands come into play as well for the nearshore assemblage. Laminar flow occurs at certain combinations of current speeds and island diameters; in laminar flow, the impinging current separates around the island and its entrained boundary layer. Thus, in gentle flows, there may be a boundary layer with little movement of water and moderately sized areas of very limited water movement ("stagnation points") both upstream and downstream (Hamner and Hauri, 1981; Fig. 1B). With increasing current flow, the thickness of this boundary layer decreases until a critical point is reached at which flow becomes turbulent. As a result, the distribution of nearshore assemblages around islands is not expected to be uniform. Regional differences in species composition (Leis, 1986b; Boehlert et al., 1992) may be a result. Thus, current speed, proximity to bottom boundaries, bottom type or roughness, and island morphology may all affect the maintenance of nearshore assemblages.

Factors important in the formation of neritic assemblages include attributes of adult spawning, passive aggregation of positively buoyant eggs, and behavior of larvae (Table 1). Fish eggs may be advected to localized areas, providing an aggregation mechanism from more spatially dispersed spawning (see summary in Shapiro et al., 1988). Passive concentration of positively buoyant eggs into windrows may later result in concentrations of larvae. This is best demonstrated for the buoyant eggs of corals (Wolanski et al., 1989; Black et al., 1990) but is not well documented for fish eggs. The distribution of fish eggs in the downstream, neritic region around Johnston Island (Boehlert et al., 1992), however, suggests that it may occur. Egg abundance in the upper 50 m of the water column showed highest densities downstream of the island (and in particular at a single station) in a moderately high background density (nearly 200 eggs$\cdot$1,000 $m^{-3}$). At 50 to 100 m depth, egg abundances were high immediately downstream of the island (Fig. 6), but were nearly zero at greater distances. This suggests either that certain species spawn in deeper water near the island or that vertical mixing occurs. In the former case, the egg abundance may be due solely to spawning distribution, whereas in the latter case, passive accumulation may form and maintain the observed distribution. It is interesting to note the similarity of the egg distribution in Figure 6 to that of the neritic assemblage in Figure 5A. The dominant species (*Eviota epiphanes*) in that assemblage (Table 3) has demersal eggs, while some of the other species have pelagic eggs. Although physical mechanisms resulting in passive accumulation are not unique to oceanic islands, they may play an important role in the formation of spatially restricted neritic assemblages.

Current-topography interactions are important to neritic assemblages of larvae. Theory holds that with increases in current speed, flow becomes turbulent and a stable eddy pair can become entrained in the downstream area; upstream and downstream stagnation points may remain (Fig. 1C). The scale of the eddy pair is on the order of an island diameter. With further increases in current speed, one of the two eddies will increase in size and vorticity until it is shed downstream, followed by buildup and eventual shedding of the other eddy (Fig. 1D). Larvae

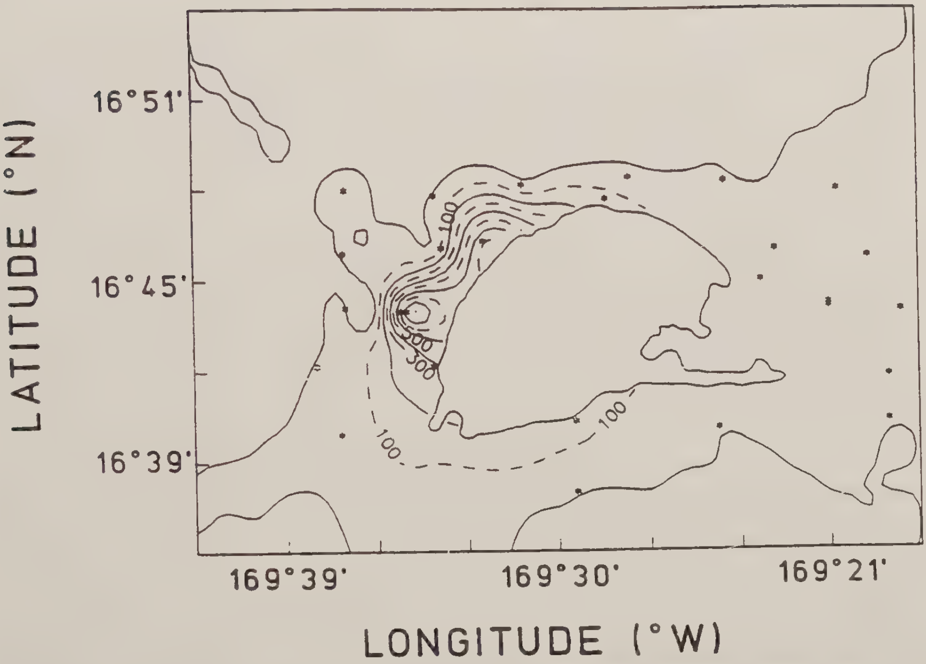

Figure 6. Distribution of fish eggs in the 50 to 100 m depth stratum around Johnston Island: the outline surrounding the island represents the 18-m isobath (from Boehlert et al., 1992). Density notations are eggs per 1,000 $m^3$.

may be retained in areas of limited water motion or in the entrained eddies. Larvae present in shed eddies will be advected from islands. Both physical and biological processes involved require more research, but they may affect the integrity and distribution of neritic assemblages.

Another theoretical mechanism that is pertinent to islands in tidally driven currents is rotary flow (Pingree and Maddock, 1985a). Observations at islands, however, are relatively limited: Pingree and Maddock (1985b) described movements of a drogue in waters surrounding a small island. Its behavior supported the predictions, with several clockwise loops around the island over a 3-day period. The relevance of this pattern to retention and maintenance of larval fish assemblages, however, is difficult to evaluate; little information was provided on the time scale of formation or retention of water masses around islands. Tidally generated eddies, however, are unlikely to remain near an island on the time scale important to recruitment (Wolanski and Hamner, 1988), and oceanic islands are typically less subject to tidal mixing and flow reversal as compared to islands on continental shelves (Bakun, 1988). The approach of Loder et al. (1988) could be beneficially applied in this situation. That is, analysis of time scales of water exchange in directions around an island (radially outward, rotary motions tangential to bathymetry, and in the vertical) would simplify highly complex flow patterns to allow interpretation of their role in biological phenomena.

The time scale of eddy retention is important to consider relative to assemblages. Downstream eddies with identifiable biological characteristics have been seen in several studies, but estimated time scales of water retention vary. Heywood and

Priddle (1987) estimate a minimum retention time of 11 days for an eddy characterized by high phytoplankton biomass observed downstream of King George Island in the Southern Ocean. Through downstream measurements of phytoplankton biomass, they suggested that only 50% of the phytoplankton was retained within the eddy during its residence at the island. Heywood et al. (1990) observed very distinct physical and biological features characterizing a trapped eddy downstream of Aldabra Atoll in the Indian Ocean, but it was absent 1 month later in slower flow conditions.

Upwelling in the lee of an island, as noted by Heywood et al. (1990), as well as along the flanks can interact with behavior to result in retention of larvae. Leis (1986b) suggested a related mechanism in the maintenance of larvae upstream of an island by upward swimming to maintain position in a downwelling feature. This is similar to proposed mechanisms of planktonic population maintenance through "winter cascading" off Bermuda (Boden and Kampa, 1953). The role of "linear oceanographic features" (Kingsford, 1990) may take many forms but, with appropriate behavior of the animals, can aggregate and potentially orient larval and juvenile fishes (Kingsford and Choat, 1986) in a landward direction. Tidally induced fronts may extend some distance (on the order of 2 km) from islands or reefs, thereby increasing the "effective size" of an island system (Kingsford et al., 1991).

Relatively little can be said about the nature of formation and maintenance of the oceanic assemblage. Eddy shedding from an island in a unidirectional current may develop a von Karman vortex street of eddies in downstream waters as observed by Barkley (1972) for Johnston Island. He suggested this wake would be detectable some 600 km downstream of that island. While this process would advect larval fish assemblages entrained in the eddy (presumably with species from the neritic and oceanic assemblages) far downstream, eddies from upstream along with their biological communities may be "trapped" by islands (Heywood and Priddle, 1987; Atkinson et al., 1990). Similarly, Dehknik et al. (1966) proposed that eddies transported oceanic larvae to the island of Cuba, as opposed to retaining larvae of nearshore species near the island.

*Interrelations Among Assemblages: Questions of Scale.*—As discussed above, the temporal and spatial bounds of ichthyoplankton assemblages around oceanic islands are poorly defined. Thus, it is difficult to evaluate the possible interrelationships among the four types of assemblages. Of the four, the spatial boundaries of the embayment and lagoon assemblage are best defined, yet little research exists on ichthyoplankton in these areas, unlike that in continental shelf islands (Leis, 1981, 1986a) or estuarine systems (Boehlert and Mundy, 1988). It is likely, however, that this assemblage has the best potential to maintain its integrity given the relative stability of the habitat and the microscale consistency of occurrence of certain species (Kobayashi, 1989). Similarly, the nearshore assemblage as defined by Leis (1978) may retain its integrity, possibly through visual orientation (i.e., bottom-oriented behavior) and use of microscale hydrographic features that may protect larvae from advection.

The neritic assemblages may be dependent upon small to mesoscale hydrographic processes and may thus be characterized by greater "leakiness" to the oceanic assemblage. Leis (1982) suggested that the neritic assemblage off Oahu may have been maintained by a small (ca. 3 km) tidally generated eddy with more stability than ocean current-generated eddies. Lobel and Robinson (1986, 1988), however, considered larger mesoscale eddies generated by local winds off the island of Hawaii as serving the same function. The scale, at some 50 to 150 km, clearly exceeds the bounds of the neritic zones as defined above, yet the dominant species observed by Lobel and Robinson (1988) are characterized as neritic in other studies (Table 2). Lobel and Robinson (1988) suggested that larvae could complete their development during the period in which the eddy remained near the island. That these eddies expand and move off to oceanic waters periodically (Patzert, 1969), however, suggests that they may carry away significant components of the neritic assemblage, which will dissipate with time into the ocean assemblage.

It would be difficult to determine the real offshore extent of the oceanic assemblage because of the rarity of larvae. Certainly larvae of shorefishes taken at vast distances from land (Victor, 1987) have a poor chance at settlement in an appropriate habitat. Given the nature of the problem and the costs of sampling on this scale, it is doubtful that significant progress will soon be made in greater definition of this assemblage.

## Summary and Conclusions

Evidence for the presence of unique ichthyoplankton assemblages is weak at best for small seamounts and equivocal at larger banks and seamounts. Some species seem to be adapted for transport of larvae away from these habitats. Seamounts may serve to disrupt oceanic ichthyoplankton assemblages through physical and biological interactions. Oceanic islands, on the other hand, have characteristic ichthyoplankton assemblages that have been described as embayment, nearshore, neritic, and oceanic. Even here, however, definition of the spatial and temporal dimensions of assemblages will require further work. The lack of identification of the assemblages by quantitative, replicated techniques means that they may only be considered as hypotheses of ecological associations. The absence of such investigations leads us to conclude our discussion of ichthyoplankton assemblages at seamounts and oceanic islands with two questions. First, "Do the proposed assemblages of fish larvae at seamounts and islands have ecological meaning?" The relationship to physical and biological factors, and the temporal and spatial robustness of island assemblages, require further attention before this can be answered. Second, "What role do these assemblages play in the maintenance of potential recruits in the two habitats?" Understanding this role may lead to improvements in our approach to dealing with questions of settlement and recruitment in seamount and oceanic island ecosystems.

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# METHODS FOR ANALYZING INTERACTIONS OF LIMITED-RANGE FISHERIES: HAWAII'S PELAGIC FISHERIES

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## ABSTRACT

A review of previous studies indicated that local fishing intensity can affect local pelagic fish abundance, but overall abundance on a wider scale may have a greater local effect. Interactions of limited-range fisheries were explored using a theoretical model in which local catch per unit effort (CPUE) declines as the catch approaches or exceeds the rates of fish immigration and recruitment in a limited area. The model has the local catch increase with effort to an asymptotic level. This simple model was used to simulate local CPUE in relation to varying rates of immigration and local fishing. Simulated data were used to test an analytical approach--the regression of CPUE on catch--which was then applied to real data from Hawaii's troll fishery. Analyzing CPUE in relation to catch rather than effort was convenient because fishing effort is poorly documented in Hawaii and includes effort by diverse methods. The analysis indicated that the CPUE of yellowfin tuna (*Thunnus albacares*) in Hawaii's troll fishery was not affected significantly by total yellowfin tuna catch in Hawaii in 1987-90, but was directly related to an index of abundance for surface-caught yellowfin tuna in the western Pacific.

## 1. INTRODUCTION

In Hawaii and in many Pacific island nations, locally-caught pelagic fishes constitute a small fraction of stocks that extend far beyond the range of the local fisheries. Primary concern over the status of these stocks is appropriately focused on abundance and production throughout their range (Suzuki, 1989). However, the rate of replacement of fish within any area is finite. Theoretically, if fishing mortality in an area increases greatly in relation to net immigration and recruitment, local catch per unit effort (CPUE) will decline. If there are several fisheries in such an area, fishery interactions may occur.

Fishery production models, which typically are used to estimate maximum sustainable yields for pelagic species (Suzuki, 1989; IATTC, 1992), are not very useful for detecting fishery interactions. Nor are they useful for estimating the optimal level of fishing effort in localized fisheries that are too small to significantly affect the size of the stock or its level of production (Sathiendrakumar and Tisdell, 1987). In many areas of the Pacific, including Hawaii, tropical tuna and billfish production may be limited mostly by immigration from surrounding areas rather than by the reproduction and growth of resident fish. For such fisheries, a model in which the local catch increases with effort towards an asymptote was proposed by Sathiendrakumar and Tisdell (1987).

In this paper, I develop a simple model for the relationship between catch and effort in a limited-range fishery on a highly mobile pelagic stock. The model is similar to that of Sathiendrakumar and Tisdell (1987) but is explicitly formulated as a function of immigration, emigration, natural mortality, and catchability. I use the model to simulate data for a fishery in which immigration, emigration, and fishing effort are seasonal. The simulated data are used to test whether the effect of fishing intensity on local catch rates can be adequately quantified by regressing CPUE on catch rather than on effort. Using catch rather than effort to quantify fishing intensity is helpful if total fishing effort is poorly documented and derived from widely different fishing methods, as is the case in Hawaii. Finally, the CPUE in Hawaii's troll fishery for yellowfin tuna (*Thunnus albacares*) is analyzed in relation to the total catch by troll, handline, and longline fisheries to determine whether the troll CPUE has been affected by total fishing intensity.

## 2. REGULATING LOCAL FISHING EFFORT IN HAWAII

Local fishery managers in the USA Exclusive Economic Zones (EEZs) of the central and western Pacific can do little about the distant-water foreign fisheries, which operate outside the EEZs and harvest the majority of pelagic fish caught in the region (NMFS, 1991). The primary USA fishery-management objective is to prevent recruitment overfishing (NMFS, 1989), defined in relation to pelagic populations which are mostly exploited beyond USA jurisdiction. This objective is dysfunctional, since there exists no international management organization through which stock-wide objectives can be achieved (NMFS, 1991). Therefore the USA Western Pacific Regional Fishery Management Council (WPRFMC) has focused its objectives on "equitable domestic utilization of the resources. . ." among user groups (WPRFMC, 1991). Recognizing that the domestic catch within the EEZs of the USA may be large enough to reduce local CPUE and cause local fishery interactions, the WPRFMC has attempted to regulate fishing effort in Hawaii's EEZ (WPRFMC, 1991).

Recent increases in the total catch of pelagic species in the USA Pacific EEZs have mostly been due to an expanding domestic longline fishery in Hawaii (Ito, 1991; WPRFMC, 1991). The less mobile, small-vessel troll and handline fisheries in Hawaii have experienced declines in total catch and CPUE (Boggs, 1991) as the longline fishery has expanded. Concern by troll, handline, and longline fishermen over reduced CPUE, together with gear conflicts, dangerous confrontations between fishermen, and overcrowding of dock facilities, induced the WPRFMC to pass regulations halting the entry of additional vessels into the USA domestic longline fishery in Hawaii in 1990. To prevent gear conflicts, the WPRFMC in 1991 also passed regulations closing nearshore areas (<50-70 miles, depending on location) to longline fishermen.

Scientific evidence in support of limiting longline-fishery participation in Hawaii has been sparse. Prior to 1986 the WPRFMC focused on the impacts of foreign longline fishing within Hawaii's EEZ on catch rates for pelagic management unit species (PMUS) which included billfish, mahimahi (*Coryphaena hippurus*), wahoo (*Acanthocybium solandri*), and pelagic sharks, but not tunas (Lovejoy, 1977, 1981; Wetherall and Yong, 1983; Skillman and Kamer, 1992). The possible impacts of foreign fishing in the EEZ were regulated by the original Pelagic Fisheries Management Plan (WPRFMC, 1986) but became irrelevant as no foreign longliners exercised the option to fish legally in Hawaii's EEZ after 1980. However, the expanding domestic longline fishery in Hawaii now catches more fish than the foreign longliners did before 1980 within the EEZ (WPRFMC, 1991). This catch increase, plus the inclusion of tunas as a Pacific Pelagic Management Unit Species (PPMUS) in 1992, provided some impetus to regulate the domestic fisheries.

Regulating fishing effort rationally requires a quantification of the effect of local fishing pressure on local CPUE for pelagic species, and a means of choosing a desirable level of fishing effort. An optimal level of fishing effort can be estimated if the cost of effort and the value of catch are defined and the relationship between catch and effort is quantified as an asymptotic curve (Sathiendrakumar and Tisdell, 1987). In the asymptotic catch model, although catch never declines because of overfishing, CPUE does decline as effort increases. Thus, detecting and quantifying an asymptotic relationship between local catch and fishing effort would help indicate whether regulating the local fishing effort is justified.

The optimization of fishing effort, in relation to the appropriate costs and benefits, depends on the relative mix of the fisheries comprising the total effort. Thus, the allocation of fishing effort among interacting fisheries is an additional problem. Changing the composition of effort by different gear types will alter the optimum. Furthermore, the decision as to which fishery to regulate, and how, may be strongly influenced by historical, social, or logistical considerations. For example, the least-mobile fisheries are most vulnerable to local declines in CPUE, and this could be a reason to limit the effort of the more mobile longliners in some areas rather than the effort of all the fisheries in those areas. In any case, evidence that local fishing pressure affects local CPUE should be the basis of any scheme for regulating fishing effort.

## 3. REVIEW OF PREVIOUS RESEARCH

Several previous studies suggest that localized fishing effort can reduce catch rates (CPUE) for wide-ranging pelagic stocks in a local area (Lovejoy, 1977, 1981; Wetherall and Yong, 1983; Squire and Au, 1990; Skillman and Kamer, 1992). Lovejoy (1977, 1981) simulated the pelagic fisheries in Hawaii's EEZ and predicted that small increases in the domestic catch of blue and marlin (*Makaira mazara*) and striped marlin (*Tetrapturus audax*) would result if foreign fishing in the EEZ was eliminated. Wetherall and Yong (1983) modelled blue marlin catch rates near Hawaii as a function of mid-Pacific abundance, recruitment, and fishing effort, and found that increases in local, adjacent, and mid-Pacific effort had negative impacts on CPUE near Hawaii. Skillman and Kamer (1992) found significant negative correlations between foreign longline effort and Hawaii's longline catch rates for blue and striped marlins. Most recently, Squire and Au (1990) found that local longline and troll catch rates of striped marlin rebounded when longline fishing was temporarily excluded from an area off Mexico. All of these studies found that local fishing effort affected local CPUE, but they lacked the appropriate model or sufficient data to accurately quantify the relationship, and thus provided no means of choosing an optimal intensity for local fishing effort.

The model of Lovejoy (1977) demonstrated that short-term abundance of transient populations was reduced by increasing local fishing effort, but the relative magnitude of the reduction was dependent on the actual (but unknown) number of fish in the area. Lovejoy (1977) used monthly Japanese longline CPUE data (1962-75) to model the spatial distribution, abundance, and catch of marlin in 27 subareas of Hawaii's EEZ and a single

Pacific (pooled) area. Fish movements through the EEZ were simulated to match geographic changes in Japanese CPUE in the 27 Hawaiian areas, assuming general north-south movements for blue marlin and northwest-southeast movements for striped marlin. However, the estimates of abundance and catchability were essentially guesses, and the catches predicted by the model were very sensitive to these parameters. This marlin-fishery simulation (Lovejoy, 1977) was repeated with the removal of the fishing mortality caused by longline fisheries in the EEZ (*i.e.*, set to zero). When Japanese longline fishing in the EEZ was eliminated, the changes in the fish abundance were small in areas fished by the small-vessel trollers, as were the effects of changes in abundance on troll catches of blue and striped marlins (2 and 5%, respectively). The simulated increases in troll catches were larger when domestic longline fishing also was eliminated (5 and 21%, respectively). Though smaller than the Japanese fishery in the EEZ at that time, the domestic longline fishery had a greater simulated impact because it had a greater geographic overlap with the troll fishery.

The sensitivity of the Lovejoy (1977) simulations to parameter estimates was illustrated when the estimated abundances of the marlin stocks were altered (Lovejoy, 1981). When the number of marlins moving from the Pacific-pooled area to Hawaii's EEZ was halved (Lovejoy, 1981) and catchability was increased to simulate the same catches as in the original model, eliminating all longline-fishing mortality increased the simulated troll catches of blue marlin by 13% and striped marlin by 45%, respectively. In contrast, when abundances were doubled, eliminating all longline fishing increased the troll catch of blue marlin by only 1% and striped marlin by 3%.

Exogenous factors may overwhelm the influence of local fishing effort on local catch rates of highly-mobile pelagic fish. Indices of abundance (CPUE) in local areas, for example, have been found to be significantly correlated with CPUE over a much wider range. Using Japanese longline catch-and-effort statistics for 1962-79 to compute estimates of abundance, Wetherall and Yong (1983) found that variation in blue marlin catch rates at the beginning of a year in a mid-Pacific area explained 80% of the annual variation in peak third-quarter catch rates in a 5x10 degree (latitude x longitude) area around the main Hawaiian Islands. No other statistically-significant predictors of local catch rates were found, but by including the variables for a recruitment trend and the foreign fishing effort in local, adjacent, and mid-Pacific areas, Wetherall and Yong's (1983) regression model increased the amount of accountable variation from 80% to 95%. Their analysis suggests that the impact of local effort on Hawaii's blue marlin fishery was small compared with the impact of abundance on a wider scale, under the conditions prevailing in 1962-79.

Pronounced seasonal cycles characterize the local, apparent abundance of large, tropical, pelagic species, especially towards the higher latitudes. The effect of local effort on CPUE may well depend on the season. Wetherall and Yong (1983) and Squire and Au (1990) accounted for seasonal effects by eliminating all but the data for the season of peak CPUE. Another method used by Skillman and Kamer (1992) was to decompose the seasonal and nonseasonal components of quarterly and monthly time series and examine the nonseasonal component. At a quarterly resolution, deseasonalized, local, domestic longline CPUE statistics for blue and striped marlins in Hawaii (1962-78) were significantly negatively correlated with foreign longline effort in local and adjacent areas ($P < 0.05$), whereas no significant correlation was found at the annual resolution

(Skillman and Kamer, 1992). The correlation coefficients were low (-0.26 to -0.32, nonparametric Spearman coefficients), and no attempt was made to quantify the relationships. Domestic longline CPUE statistics were most negatively correlated with Japanese longline effort in the local area, again suggesting a stronger relationship with increased proximity.

An unintended "experiment" on the effect of local fishing effort on local marlin CPUE was performed by the government of Mexico in 1977 when it enforced regulations against foreign longline fishing within its 200-mile exclusive economic zone. The enforcement caused a major decrease in fishing effort, allowing an interesting comparison to be made between catch rates before and after 1977 (Squire and Au, 1990). Striped marlin catch rates by troll fishermen in the area west of Mazatlan and around the tip of Baja California doubled during 1977-80 (Squire and Au, 1990). Joint-venture longline operations beginning in 1979-80 in the area also experienced catch rates twice as high as those in 1976. This series of events suggests a much stronger effect of local fishing effort on CPUE than that indicated for Hawaii's fisheries (Lovejoy, 1977; Wetherall and Yong, 1983; Skillman and Kamer, 1992). The opportunity to make a comparison like that of Squire and Au (1990) between CPUE statistics before and after the abatement of foreign longline fishing in Hawaii's EEZ (1980) was given as a reason for regulating foreign longline fishing (WPRFMC, 1986). Unfortunately this analysis was never undertaken, partly because of a severe decline in reporting of Hawaii's fishery statistics beginning around 1979 (S. Pooley, Honolulu Laboratory, National Marine Fisheries Service, Honolulu, HI 96822-2396, unpubl. manuscr.).

Squire and Au (1990) described the Mexico striped marlin fishery as operating in a "core area" in which fish naturally aggregate in concentrations that are much higher than throughout the population range. When they analyzed catch rates of the joint-venture fishery and the foreign longline fishery off Mexico in relation to fishing effort during 1962-84, they found no clear quantitative relationship. This was largely because the CPUE in the core area declined in 1981-84, despite relatively low levels of effort. Squire and Au (1990) suggested that a reduction in core-area fishing effort disproportionately raises the local CPUE, because core-area CPUE depends more on the formation and fishing down of "hot spots" than on stock production. Hypothetically, the relationship between fishing effort and CPUE in "hot spots" could be different from that in a larger area. Such a relationship could be demonstrated only if the data had very fine geographic resolution.

## 4. ASYMPTOTIC MODEL FOR LOCAL CATCH

A model for a local fishery in which the catches reach an asymptote as fishing effort increases was proposed by Sathiendrakumar and Tisdell (1987) to determine the optimal level of local fishing effort. I propose a similar model except that the parameters are defined in relation to immigration, emigration, mortality, and catchability. Emigration is treated as if it were analogous to natural mortality, so the two are combined. In the simplest case of this model (*i.e.*, assuming steady-state equilibrium and constant "natural mortality" and catchability), the asymptotic maximum catch is governed by the level of immigration (Figure 1). The parameters and derivation of the model are as follows (all fluxes--immigration, catch, and mortality--are annual, and numbered expressions are considered axiomatic):

$I$ = local immigration (metric tons)--analogous to biological production but independent of local biomass;

$C_i$ = catch (metric tons) at effort level i;

$f_i$ = effort ($10^3$ hooks) at level i;

$q$ = catchability ($1/10^3$ hooks) [assumed constant];

$F_i$ = fishing mortality [$F_i = qf_i$]; (1)

$M'$ = "natural mortality" including emigration [assumed constant],

$Z'_i$ = total "mortality" including emigration [$Z'_i = M' + qf_i$]; (2)

$B_i$ = equilibrium biomass (metric tons) in the local area [$B_i = I/Z'_i$]; (3)

$C_i = B_i F_i$ (metric tons); (4)

$$C_i = \frac{IF_i}{Z'_i} \text{ (metric tons)} \qquad \text{[from (3)];}$$

and

$$C_i = \frac{Iqf_i}{M' + qf_i} \text{ (metric tons)} \qquad \text{[from (2)].}$$

The example shown (Figure 1) uses arbitrary values: $I$ = 5,000, 10,000, and 20,000 metric tons, $q$ = 0.0001/1,000 hooks, and $M'$ = 0.06. When fitting the model to data where $I$, $q$, and $M'$ are unknown, the model can be simplified:

$$\text{If} \quad a = \frac{Iq}{M'} \quad \text{and} \quad b = \frac{q}{M'} ,$$

$$\text{then} \quad C_i = a\left(\frac{f_i}{1+bf_i}\right) \text{ (metric tons).}$$

Algebraic manipulation of the model equation yields the following linear relationship between CPUE and catch (Figure 2):

$$\frac{C_i}{f_i} = a - bC_i \quad \text{(metric tons/10}^3\text{ hooks)},$$

which makes the model easy to fit.

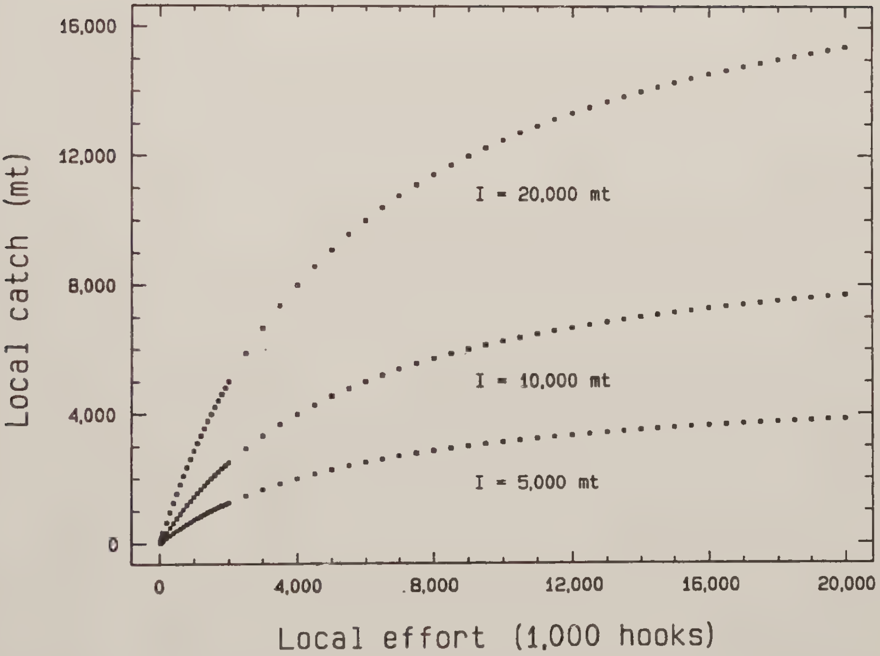

Figure 1. Asymptotic catch model for a limited-range pelagic fishery that catches a small fraction of the stock of a highly-mobile pelagic species. Natural mortality, emigration, and catchability are constant, and the local biomass of fish is at equilibrium. Annual immigration (I) determines the annual asymptotic catch in metric tons (mt).

Unfortunately, in reality, immigration, emigration, and effort vary seasonally, and equilibrium is not achieved instantaneously. A more realistic model was created by making immigration, natural mortality (plus emigration = $M'$), and fishing effort vary according to annual cycles, with effort also increasing over time. Simulated data were obtained by calculating the catch, mortality, and the resulting nonequilibrium local biomass at 10 time steps per day for 4 years, summarized by month (Figure 3). The annual cycles of immigration and emigration were chosen to produce a cycle of local biomass roughly resembling the pattern seen in CPUE data from Hawaii's yellowfin tuna fisheries.

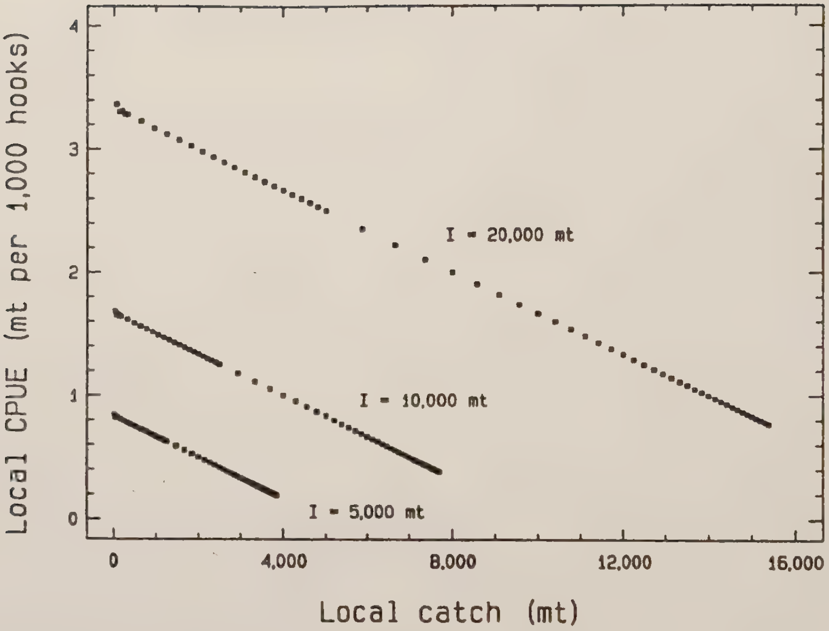

Figure 2. Relationship between local CPUE and total local catch in metric tons (mt) according to the asymptotic catch model in Figure 1.

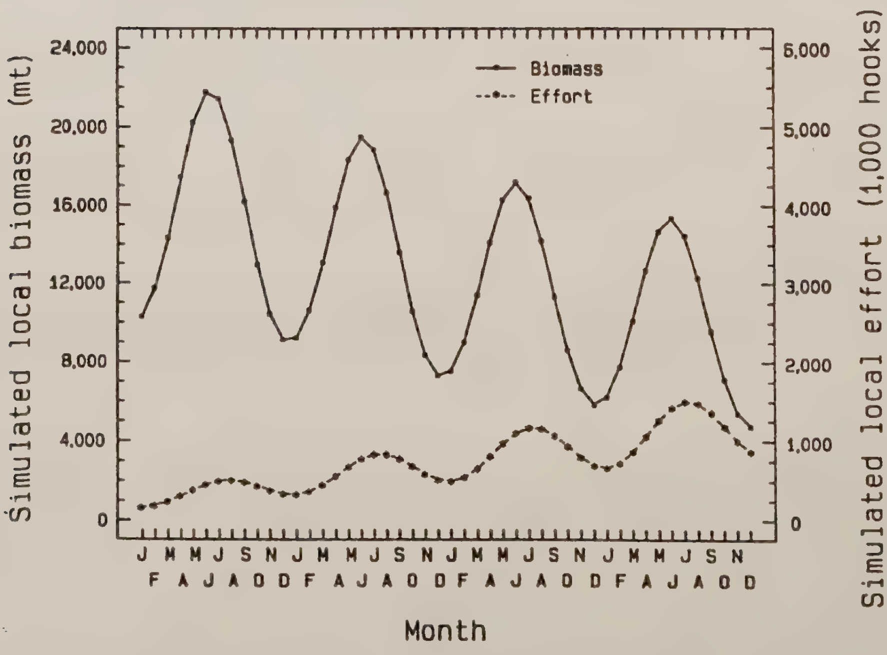

Figure 3. Simulated monthly biomass in metric tons (mt) and fishing effort in a limited-range fishery like that in Hawaii. Immigration, emigration, and effort vary in an annual cycle, and effort increases threefold over 4 years. Local biomass is not in equilibrium.

When the simulated CPUE data and catch are plotted, there is a clear relationship between CPUE and catch, although the slope is different for each month of the year (Figure 4) in keeping with the monthly changes in $I$, $M'$, and $F$. The nonlinearity of relationships for each month is due to lag effects under nonequilibrium conditions (the nonlinearity disappears when CPUE for each month is plotted *versus* catch for the 5-month period ending that month). Ignoring the nonlinearity, multiple regression of seasonally-adjusted CPUE on catch and first-order interactions between catch and months explains 96% of the variance in the simulated data, suggesting that this simple analytical approach could work with real data. However, the simulated data contain no random components which might obscure weak relationships.

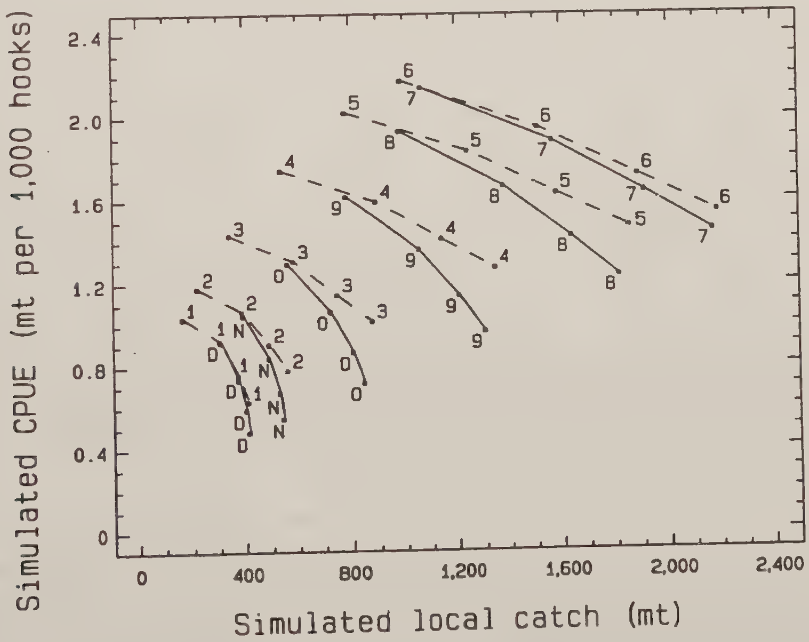

Figure 4. Simulated local catch per unit effort (CPUE) plotted versus simulated local catch in metric tons (mt) for the limited-range fishery model with seasonal variation and increasing effort as in Figure 3. Relationships between CPUE and catch for the first (dashed lines) and last (solid lines) 6 months of each year are identified by characters (1-9 for January-September, and O, N, D for October, November, and December, respectively).

Further realism was added by making immigration vary annually as well as seasonally. When immigration was reduced by 40% in alternate years, the resulting relationship between simulated CPUE and catch was hard to perceive (Figure 5). However, using a dummy variable (1 or 0) for high and low immigration years (and including first-order interactions between immigration and months) made it possible to use multiple regression to describe the slopes and intercepts of the CPUE- *versus*-catch relationships for each month and level of immigration (Figure 5). These slopes and intercepts were then used to compute the asymptotic relationships between catch and effort (Figure 6).

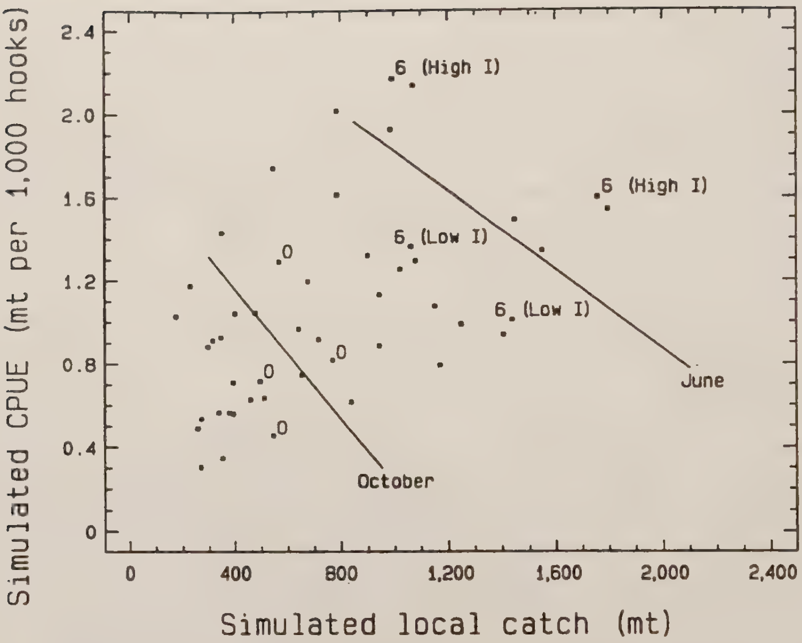

Figure 5. Simulated local catch per unit effort (CPUE) plotted versus simulated local catch in metric tons (mt) for the limited-range fishery model with immigration (I) alternating from high to low (40% less than high) in alternate years. Relationships for an average amount of immigration, calculated with the multiple regression analysis are shown for June (points labelled 6) and October (points labelled O).

In reality, local immigration is an unknown quantity, but the apparent abundance of fish over a larger area can be used as an index of immigration in a multiple regression analysis of real data. It is logical that more fish would immigrate in years when they are more abundant in the surrounding area, and this behaviour would be consistent with work showing strong correspondence between the apparent abundance of pelagic fish in local areas and abundance on a wider scale (Wetherall and Yong, 1983; Squire and Au, 1990; Skillman and Kamer, 1992). Another mechanism that would explain the correspondence in apparent abundance would be widespread changes in catchability. In contrast, changes in immigration or local catchability due to localized environmental conditions would not be consistent with the observed correspondence in apparent abundance, and thus the local environment may represent an additional source of variation.

The simulations illustrate how relationships between catch and effort within a limited area may differ seasonally and annually. The optimal level of fishing effort may be highly dynamic, making the rational management of fishing effort difficult. Analyzing CPUE data *versus* catch should at least be useful for detecting an impact of local fishing pressure on local CPUE, even when that impact differs seasonally and annually. Detecting such an impact however may require quantifying variation due to other factors.

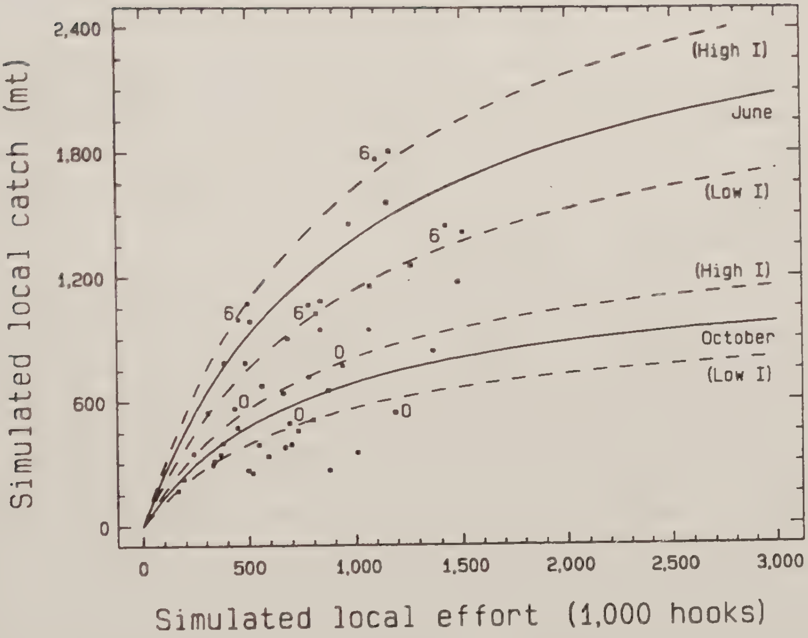

Figure 6. Asymptotic catch relationships for monthly local catches in metric tons (mt) as a function of monthly local effort in a limited-range fishery from the analysis of simulated data shown in Figure 5. The relationships for high and low immigration (I) years (dashed lines) differ from the average relationship (solid lines) for each month (June data labelled 6; October data labelled O).

## 5. YELLOWFIN TUNA CPUE IN HAWAII

In a preliminary study (Boggs, 1991), troll and handline CPUE data (pounds per trip) were plotted *versus* longline catch to determine whether relationships appeared that might be indicative of fishery interactions. This graphical inspection of the CPUE *versus* catch data was applied to yellowfin tuna, bigeye tuna (*Thunnus obesus*), blue and striped marlins, mahimahi, and wahoo. In the preliminary study (Boggs, 1991), the analyses covered data for January 1987-June 1990. The present study extends the analysis through the end of 1990 for yellowfin tuna troll CPUE (pounds per trip) and compares troll CPUE with the total catch (by all fisheries) rather than just the longline catch.

The data used to calculate troll catch per trip (CPUE) were provided by the Hawaii Division of Aquatic Resources (HDAR) as summaries of commercial catch (pounds of fish) by year (1983-90) and month (1987-90) along with summaries of the total number of fishing trips per year or month, respectively. Annual and monthly catch rates were calculated as the ratio of total catch (in pounds) to the number of trips. No geographic categorization of the data was used, but most of the troll fishing was conducted within 50 miles of shore around the eight main Hawaiian Islands. The HDAR catch data did not contain reports of trips; rather, each date for each vessel in the records was counted as a trip if any PMUS or tuna was reported caught. The assumption of 1-day trips is fairly realistic for the small-vessel troll and handline fisheries.

Catch per trip may not be a good measure of yellowfin tuna abundance since important operational changes and improvements in trolling methods have undoubtedly occurred over the years. The catch per trip index contains no data from trips with zero catches, no standardization of trips as a unit of effort, no estimate or correction for underreporting, and no estimate or correction for changes in reporting over time. Any of these factors could bias trends or relationships in the data, or give the appearance of a trend or relationship where none exists.

Despite these potential problems, catch per trip as an abundance index can provide some indication of changes in the local abundance or availability of fish to trollers and handliners in Hawaii. Catch per trip indices based on HDAR data often mirror patterns seen in more sophisticated CPUE indices, such as catch per hook or catch per set, from nearby fisheries (Wetherall and Yong, 1983; Skillman and Kamer, 1992). When the data from several different sources show a similar pattern, those data probably indicate a true pattern of apparent abundance unless some unknown bias affects several sources of data similarly. In any case, catch per trip is the only available measure of CPUE for Hawaii's troll and handline fisheries. More definitive examinations of trends in CPUE will require data that more accurately specify fishing effort.

Annual troll CPUE (pounds per trip) for yellowfin tuna declined from a relatively high level in 1979 to low levels in 1982-84 (WPRFMC, 1991). Troll CPUE for yellowfin tuna returned to high levels in 1987, dropped again and remained low through 1989, and showed some recovery in 1990 (Boggs, 1991). The decline in troll CPUE for yellowfin tuna in 1987-1989 corresponded with a period of dramatic expansion of Hawaii's domestic longline fishery (Boggs, 1991; Ito, 1991; WPRFMC, 1991), suggesting that some fishery interactions may be occurring. The low troll CPUE seen in 1982-84, however, occurred before the domestic longline fishery expanded and after the foreign longliners ceased fishing in Hawaii's EEZ, suggesting that periods of low troll CPUE may be unrelated to longline fishing effort.

The total longline catch, as estimated by the National Marine Fisheries Service (NMFS) shoreside monitoring programme, showed increasing monthly variation and an upward trend from 1987 through 1989, levelling off somewhat (annual average) in 1990 (Figure 7). The longline catch estimates were for the entire range of the longline fishery, mostly within the Hawaii EEZ but extending beyond it. The range of the troll and handline fisheries is much smaller and is roughly centred within the area fished by the longline fishery (these data precede the establishment of nearshore area closures for longline fishing).

The NMFS data rather than the HDAR data were used to estimate longline catch because they cover most of the longline catch in Hawaii, whereas the HDAR data cover only a small fraction of that catch. Conversely, the NMFS market sample data cover only a fraction of the troll and handline catch and do not distinguish between these two gear types, which have markedly different catch rates. Therefore to obtain total catch, the HDAR data on the catch by gear other than longline (mostly troll and handline) were combined with NMFS estimates of the longline catch. A potentially large component of

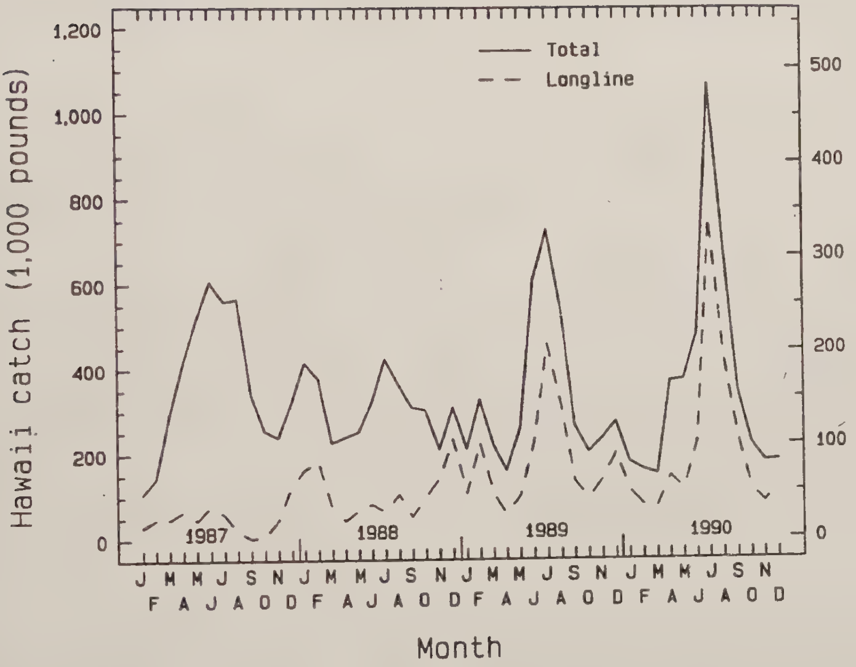

Figure 7. Total catch (all gear types combined, in pounds and metric tons) and longline catch of yellowfin tuna in Hawaii each month in 1987-90. Longline catch is estimated from the shoreside monitoring programme of the National Marine Fisheries Service, and the remainder of the total is from the non-longline catches in the commercial catch reports of the Hawaii Division of Aquatic Resources. The recreational catch is not known.

the total catch, namely the recreational catch, remains unquantified, and there are no good estimates of under-reporting by commercial troll and handline fishermen. Thus, total catch is known with less certainty than longline catch, which was one reason Boggs (1991) used only longline catch.

The total catch of yellowfin tuna by all gear types (Figure 7) varied monthly in 1987-90 but did not show much of an annual trend. As catch by the longline fishery increased, catch by the other fisheries decreased. Fishermen have suggested that increased longline catch might be causing the decline in troll and handline catch; this is why troll and handline CPUE was plotted *versus* longline catch in Boggs (1991). However, examination of CPUE in relation to total catch is more appropriate since the catch by trollers and handliners would also be expected to contribute to any local reduction in biomass.

Hawaii's trollers, handliners, and longliners depend on the same size range of fish to provide the bulk of their yellowfin tuna catch, so interactions of these fisheries are possible. Even though the troll and handline size-frequency distribution (combined) includes more small (<50 lb) fish than the longline size-frequency distribution (Ito, 1991), the small fish add relatively little to the weight of troll and handline landings (Figure 8). The combined troll and handline data (Figure 8) are mostly from Oahu where trolling predominates. Handline-caught fish tend to be even more similar in size to longline-caught fish. The reason for the decreasing catch of small fish (Figure 8) is not known.

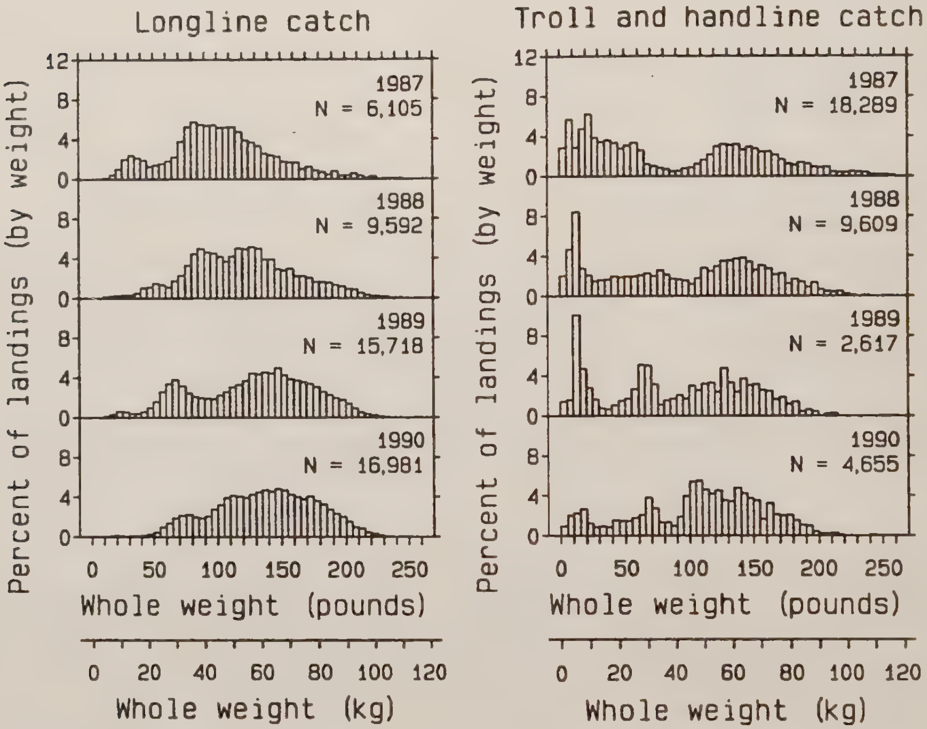

Figure 8. The proportional landings (percent of total weight landed) by weight category (pounds and kg) in Hawaii's longline and combined troll and handline fisheries. Weights of fish were obtained by the National Marine Fisheries Service shoreside monitoring programme (N = number of fish). The combined troll and handline samples are from Oahu, where trolling is the predominant small-vessel pelagic fishing method.

Changing operational characteristics in recent years make longline trips a poor measure of effective effort. For the same reason, longline-catch per trip is a poor measure of yellowfin tuna abundance and thus has not been examined. Troll and handline trips differ from each other and from longline trips in their relative effectiveness, making total effective effort difficult to estimate. Thus, total catch, rather than effort, was used as a more convenient estimate of fishing pressure.

In the preliminary analysis by Boggs (1991) of the monthly data from 1987 to June 1990, six species were examined, but only yellowfin tuna had CPUE values that appeared to be negatively related to longline catch. The relationship was clearest when monthly CPUE was plotted *versus* longline catch for the 3-month period ending the same month. Months were categorized by Boggs (1991) as "in-season" and "nonseason" to account for seasonal effects, whereas the present study used multiple regression analysis of seasonally-adjusted CPUE data on catch with interaction terms for each month.

The apparent relationship found in the preliminary study may have been due to chance, since very low troll and handline catch rates were also observed in 1982-84, well before the longline fishery expanded. Unfortunately, good estimates of total catches for the earlier period are not yet available. Estimates for this earlier period may be developed if market data from this period can be obtained from fish dealers.

When the troll CPUE data for the 48-month period from 1987 to 1990 were analyzed in relation to total monthly yellowfin tuna catch in the present study, no relationship was apparent (Figure 9). An analysis of handline CPUE gave similar results. As in Boggs (1991), the CPUE data for each month were also analyzed in relation to longline catch, and longline catch for the 3-month period ending that month, but still no relationship was found. This was due to the addition of 6 months of new data from 1990, wherein the CPUE increased over 1989 levels despite continued high levels of longline catch (Figure 10).

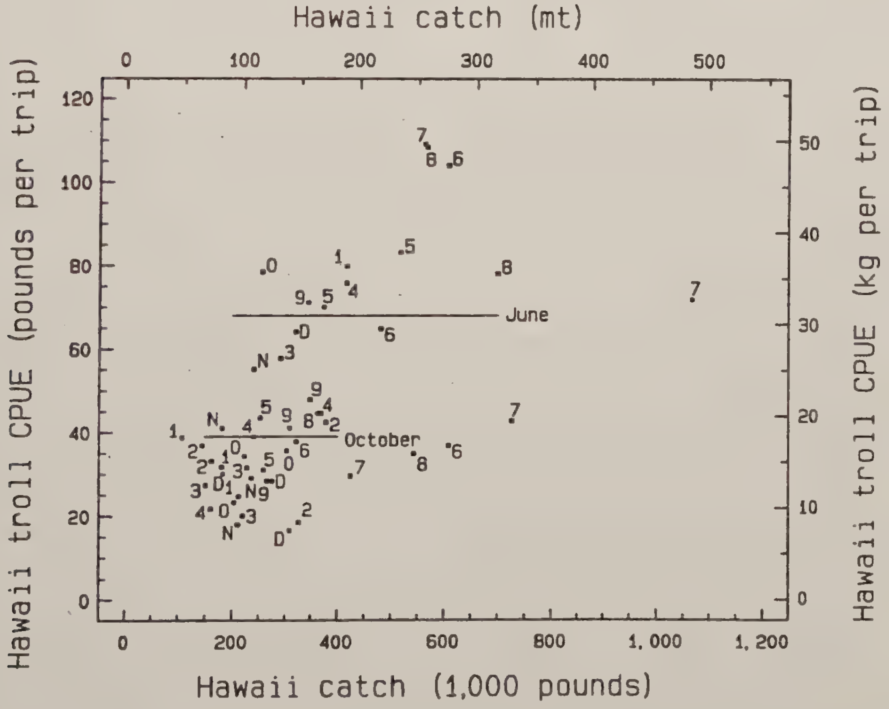

Figure 9. Observed monthly yellowfin tuna catch per unit effort (CPUE) (pounds per trip and kg per trip) in Hawaii's troll fishery, versus total monthly yellowfin tuna catch by all fishing gears (labelled as in Figure 4) for 1987-90. The lack of any CPUE versus catch relationships (slopes ≈ 0) based on multiple regression analysis is shown for June and October.

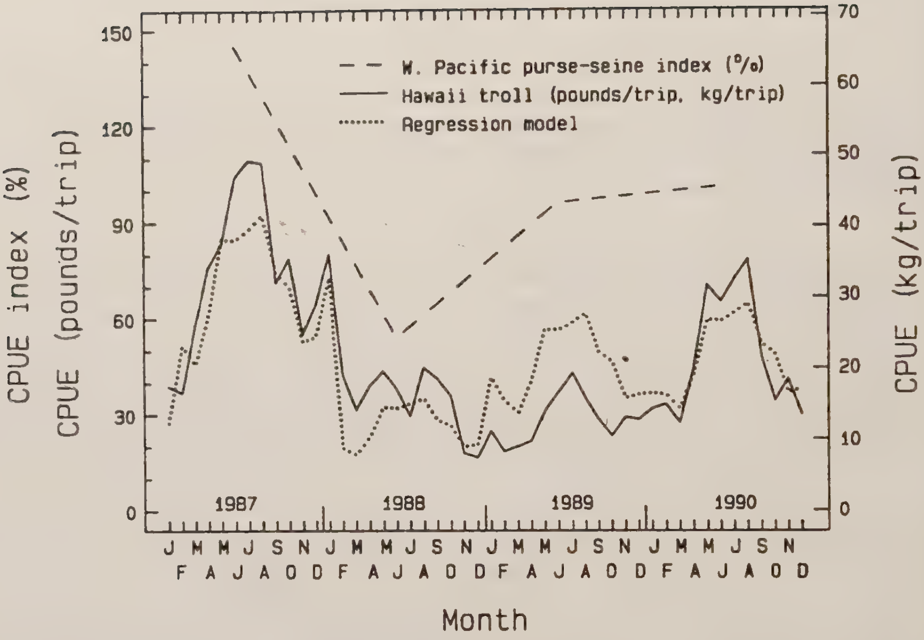

Figure 10. **Observed catch per unit effort (CPUE) (pounds per trip and kg per trip) for yellowfin tuna by Hawaii's troll fishery for each month in 1987-90, and the annual index of wide-scale abundance of yellowfin tuna from the USA and Japan purse-seine fisheries (percent of average CPUE). Predicted local CPUE from a regression of seasonally-adjusted CPUE on the purse-seine index is also shown.**

An index of wide-scale surface yellowfin tuna abundance from purse-seine fisheries in the western Pacific (Figure 10) was added to the regression analysis to see whether removing some of the interannual variation in immigration would reveal an underlying relationship between local CPUE and fishing intensity. The purse-seine index was calculated as the geometric mean of CPUE from the USA (Coan, 1993) and Japan (Suzuki, 1992) purse-seine fisheries in the western Pacific, expressed as a percent of mean CPUE (Figure 10). This index was the most significant factor ($P < 0.0001$) in a multiple regression of seasonally-adjusted local CPUE on total catch, the purse-seine index, and first order interactions by month.

Catch was not a significant factor (slope ≈ 0, Figure 9). The predicted CPUE, based on the seasonal adjustment and regression analysis, followed the pattern of observed CPUE fairly well (Figure 10). It seems that seasonality and the exogenous supply (*i.e.*, the immigration rate) of yellowfin tuna are the dominant factors affecting local CPUE, and the available evidence suggests that local CPUE was independent of local levels of exploitation in 1987-90.

It should also be noted that the purse-seine index may not necessarily represent increases in wide-scale biomass or increased local immigration. Instead it may reflect a widespread change in catchability caused by environmentally-induced changes in behaviour and vulnerability to fishing gear.

There is clearly a need for more research on the local distribution dynamics of tropical pelagic species. Simulation models could be much more helpful if more was known about true abundance and fish-movement dynamics. Tagging studies would be a good way to get such information, if they coincide with improved fisheries data collection emphasizing the geographic distribution of fishing effort and catch. The results of previous studies make it clear that local fisheries data alone may not provide evidence of existing fisheries interactions, because of the important effects of exogenous factors such as changes in stock-wide abundance and catchability. Environmental influences on fish movements and catchability may also play an important role that must be investigated.

## 6. ACKNOWLEDGMENTS

The NMFS data summaries for this study were provided by Sam Pooley (NMFS Honolulu Laboratory), and the HDAR data summaries were provided by Reggie Kokubun (State of Hawaii Department of Land and Natural Resources) and Reese Tokunaga (NMFS Honolulu Laboratory).

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# Hawaii's Pelagic Fisheries

CHRISTOFER H. BOGGS and RUSSELL Y. ITO

*ABSTRACT—Hawaii's diverse pelagic fisheries supply the bulk of the State's total catch. The largest Hawaii fishery is the recently expanded longline fishery, which now lands about 4,400 metric tons (t) of broadbill swordfish,* Xiphias gladius; *1,500 t of bigeye tuna,* Thunnus obesus, *and 3,000 t of other pelagic species annually. The increased catch of these other species has raised concerns regarding the continued availability of yellowfin tuna,* T. albacares; *blue marlin,* Makaira mazara; *and mahimahi,* Coryphaena hippurus, *in the small-vessel troll and handline fisheries which target those species.*

*Analysis of catch per unit effort (CPUE) statistics from Hawaii's fisheries did not provide strong evidence of recent declines in availability related to local fishery expansion. A more influential factor was variation in Pacific-wide CPUE, representing overall population abundance and catchability. Exogenous factors, including Pacific-wide fishing pressure, may overwhelm the influence of local fishing pressure on fish availability.*

## Introduction

Hawaii's pelagic fisheries are small in comparison with other Pacific pelagic fisheries (NMFS, 1991), but they are the largest fisheries in the State (Pooley, 1993b), and much larger than other U.S. island-based fisheries in the western Pacific (Hamm et al.[1]). Stocks of tuna, billfish, and other tropical pelagic species supply most of the fish consumed by Hawaii residents and support popular recreational fisheries.

In recent years (1987–91) the composition and magnitude of Hawaii's commercial pelagic fisheries have changed. The longline fishery greatly expanded and the troll, handline, and pole-and- line fisheries declined (Ito[2]). The expansion of the longline fishery was consistent with fishery development plans that viewed pelagic fish resources as underexploited (State of Hawaii Division of Aquatic Resources (HDAR) 1985). Pelagic fish resources available to Hawaii fisheries may be capable of sustaining even greater yields. However, the decline of the troll and handline fisheries has raised concerns regarding the continued availability of pelagic species and local overfishing (Boggs[3], Ito[2]).

Pelagic fish availability is synonymous with local abundance, here defined as the amount of fish present within the range of the local fishery. Overall abundance refers to population size, which is greater than local abundance unless the entire population resides within range of the local fishery. The stock structure of large pelagic species is unclear, but a common assumption is that pelagic populations extend over much wider areas than are covered by Hawaii's fisheries (Skillman, 1989a, 1989b; Suzuki, 1989, In press; Miyabe, In press).

Availability probably depends on overall abundance, but the availability of fish to Hawaii's pelagic fisheries is also highly seasonal (Shomura, 1959; Yoshida, 1974; Skillman and Kamer[4]), suggesting that highly mobile pelagic fish change their distribution in response to environmental conditions (Seckel, 1972; Mendelssohn and Roy, 1986), or to enter different areas for reproduction. Availability may also be confounded with catchability, defined as the vulnerability of fish to being caught by a given type of fishing gear. Catchability is also influenced by environmental conditions (Sharp, 1978; Hanamoto, 1987).

The limited mobility of most island fishermen causes yield to be poor when availability is low. Intense local fishing effort is not likely to cause a decline in overall abundance unless there are discrete stocks residing in, or periodically returning to, island waters. Otherwise, the fishing mortality caused by Hawaii fisheries is minor compared with overall fishing mortality caused by larger Pacific fisheries. Thus, local fishing pressure is unlikely to cause a significant reduction in overall abundance.

Even though locally exploited pelagic stocks may be wide-ranging, and relatively invulnerable to local fishing pressure, catch per unit effort (CPUE) in local fisheries may decline if local fishing effort is so intense that most

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[1] D. C. Hamm, R. S. Antonio, and M. M. C. Quach. 1992. Fishery statistics of the western Pacific. Vol. VII. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Honolulu Lab., Southwest Fish. Sci. Cent. Admin. Rep H-92–06, var. pag.

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[2] R. Y. Ito. 1992. Western Pacific pelagic fisheries in 1991. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Honolulu Lab., Southwest Fish. Sci. Cent. Admin. Rep. H-92-15, 38 p.

[3] C. H. Boggs. 1991. A preliminary examination of catch rates in Hawaii's troll and handline fisheries over a period of domestic longline fishery expansion. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Honolulu Lab., Southwest Fish. Sci. Cent. Admin Rep. H-91-05, 62 p.

[4] R. A. Skillman and G. L. Kamer. 1992. A correlation analysis of Hawaii and foreign fishery statistics for billfishes, mahimahi, wahoo, and pelagic sharks, 1962–78. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Honolulu Lab., Southwest Fish. Sci. Cent. Admin. Rep. H-92-05, 44 p.

fish entering the local area are soon caught. It is hypothesized (Sathiendrakumar and Tisdell, 1987; Boggs, In press) that if fish availability depends on immigration, increases in local fishing effort result in an asymptotic yield, beyond which further increases in local effort do not increase the catch, and local CPUE declines. The possible impact of local fishing effort on the CPUE and profitability of Hawaii's pelagic fisheries is currently an issue of great concern to Hawaii's fishery managers (Boggs[3], In press).

This paper describes Hawaii's longline, troll, and handline fisheries for pelagic species, trends in landings and CPUE over time, and problems with the data used to monitor these fisheries. Changes in the apparent relative availability of fish (local CPUE) are reviewed in relation to local fishery expansion and overall abundance (Pacific-wide CPUE). Current attempts at managing for optimum yield and the outlook for these fisheries are described. The Hawaii skipjack tuna fishery is covered in a separate paper (Boggs and Kikkawa, 1993).

## Synopsis of the Fisheries

The fishing methods, target species, vessel sizes, yields, and operational areas of Hawaii's domestic pelagic fisheries are diverse. The commercial sectors are largely composed of the pole-and-line and longline fisheries utilizing large (>12 m) vessels. The small-vessel troll and handline fisheries include poorly differentiated commercial, recreational, and subsistence components. The pole-and-line fishery targets skipjack tuna, *Katsuwonus pelamis,* and lands about 1,000 metric tons (t), (2.2 million lb) annually for sale to the local market (Boggs and Kikkawa, 1993). The longline fishery targets broadbill swordfish, *Xiphias gladius;* and bigeye tuna, *Thunnus obesus*, and now lands about 9,000 t (20 million lb, including all species) much of which is exported. The commercial, recreational, and subsistence troll and handline fleets primarily target yellowfin tuna, *T. albacares*; mahimahi, *Coryphaena hippurus*; and blue marlin, *Makaira mazara*; annual commercial landings (all species) now average about 2,300 t (5.2 million lb). No valid estimates exist for current recreational or subsistence landings (Pooley, 1993a).

Up until 1980 distant-water longliners from Japan caught between 1,300 and 5,000 t of tuna and billfish annually within the Exclusive Economic Zone (EEZ) around Hawaii (Yong and Wetherall, 1980) but since 1980 there has been no legal foreign longline fishing conducted in the EEZ. The Fishery Management Plan (FMP) enacted by the Western Pacific Regional Fishery Management Council (WPRFMC) was designed to regulate billfish catches by these foreign distant-water longliners (WPRFMC[5]). The Japanese distant-water pole-and-line fishery for skipjack tuna that operated in the Northwestern Hawaiian Islands (NWHI) through 1992 was the only foreign fishery operating legally within the EEZ after 1980 (Boggs and Kikkawa, 1993).

Although the primary target species of the domestic longline fishery are different from those of the troll and handline fisheries, the longline fishery also catches about 1,300 t (2.8 million lb) of yellowfin tuna, blue marlin, and mahimahi (combined). This creates a potential for fishery interaction between the longline and small-vessel troll and handline fisheries. Potential interactions, impacts on endangered species, the possibility of localized overfishing, and gear conflicts (Pooley, 1990) prompted the WPRFMC to establish regulations for the domestic longline fishery in 1990 (Dollar and Yoshimoto[6]). A moratorium on entry of longline vessels into the Hawaii fishery and prohibited areas for longline fishing were established in 1991.

## The Longline Fishery

### Fishing Methods

Longline fishing gear consists of a main line strung horizontally across 1–100 km of ocean, supported at regular intervals by vertical float lines connected to surface floats. Descending from the main line are branch lines, each ending in a single, baited hook. The main line droops in a curve from one float line to the next and bears some number (2–25) of branch lines between floats. Fishing depth depends on 1) the lengths of the float lines and branch lines, 2) the sag in the main line, and 3) the position of the branch line, the deepest branch line positions being in the middle of the droop. Fishing depth affects the efficiency with which different species are captured (Hanamoto, 1976, 1987; Suzuki et al., 1977; Boggs, 1992).

One longline "set" is made per day of fishing, and for long main lines the deployment and retrieval may take almost 24 hours. Often the end of the line deployed first is retrieved last, so individual hooks may fish for a few hours, or all day (average ca. 12 hours). Traditionally the gear was set so that it fished primarily during daylight. For bait, Hawaii longliners used locally caught scad, *Decapterus* and *Selar* spp.; imported squid, *Loligo* sp.; sardines, *Sardinops caerulea*; herring, *Clupea pallasi*; and saury, *Cololabis saira*.

The Hawaii longline fishery began in 1917 off Waianae, Oahu, using techniques imported from Japan. Hawaii longline vessels evolved from the wooden sampan-style baitboats used in the pole-and-line fishery for skipjack tuna (June, 1950). The sampans used in the early years of the fishery (ca. 1950) were 12–19 m (40–63 ft) in length, high-bowed, and diesel-powered. They carried about 12 t of ice to chill an average catch of about 3 t (7,000 lb) of fish caught over an average trip of 10.5 days (June, 1950).

Old-style longlines were made of rope and composed of individual units called "baskets" named for the bamboo containers they were stowed in (June, 1950). Each basket was made

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[5] WPRFMC. 1986. Fisheries management plan for the pelagic fisheries of the western Pacific Region. Western Pacific Regional Fisheries Management Council (WPRFMC), Honolulu, HI 96813, 380 p.

[6] R. A. Dollar and S. S. Yoshimoto. 1991. The federally mandated longline fishing log collection system in the western Pacific. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Honolulu Lab., Southwest Fish. Sci. Cent. Admin. Rep. H-91-12, 35 p.

up of the float line, main line, and branch lines necessary for one segment of longline (one droop of the line). Poles with flags were attached to the floats to mark the gear, and longlining was generally referred to as "flagline" fishing.

### Historical Development and Decline

Historically, the longline fishery was the second largest commercial fishery in the state after the pole-and-line fishery. By the 1930's longliners landed most of the 1,000 t (ca. 2 million lb) of yellowfin tuna, bigeye tuna, and albacore, *Thunnus alalunga*, landed in the Territory of Hawaii (June, 1950). After a hiatus during World War II the fishery quickly recovered, landing 900 t (2 million lb) of tuna, and 700 t (1.5 million lb) of billfish and other species in 1948. Landings continued to rise, reaching a record level of 2,000 t (4.4 million lb) in 1954 (Fig. 1A). The longline fishery declined in the late 1950's through the mid-1970's to reach a similar level of landings as the commercial troll (Fig. 2) and handline (Fig. 3) fisheries.

In the early years most of the catch was reported to have been in HDAR statistical areas 2–20 n.mi. (3.7–37 km) off Waianae, Oahu, and off Kona, Hilo, and Hamakua, Hawaii (June, 1950). Shomura (1959) reported greatly improved catch rates for bigeye tuna by longline vessels fishing off the windward coasts (i.e., Hilo) in winter as opposed to the traditional practice of fishing off sheltered leeward coasts (i.e., Waianae, Kona). Hida (1966) reported a growing number of longliners extending their range 100–400 n.mi. south of Oahu, and noted that CPUE was better than average in the southern area.

The species composition of longline landings changed over time. During 1951–64, more than 50% of longline landings (by weight) were bigeye tuna, also called ahi (a Hawaiian name), ahi mebachi, or "bluefin." True bluefin tuna, *Thunnus thynnus*, are rarely caught by Hawaii fishermen. Before 1950 and in the 1970's bigeye tuna and yellowfin tuna (also called ahi) made up roughly equal proportions of the catch (Fig. 1A). The proportion of blue marlin in the catch was higher than that of striped marlin, *Tetrapturus audax*, in the early 1950's but striped marlin became more predominant from the early 1960's to the present (Fig. 1A). Both marlin species are also called au (the Hawaiian name) or "swordfish," but they should not be confused with broadbill swordfish (Fig. 1B), which became the primary target species in the 1990's (Dollar[7]). Local common names for the pelagic species are often used for reporting catch statistics, resulting in some confusion.

The decline of the Hawaii longline fishery in the late 1950's through mid-1970's was characterized by a lack of new investment. Only a few new steel or fiberglass boats were built or added to the fleet between 1950 and 1982. Only 3 out of 11 boats surveyed in 1982 were built after 1970 (Hawaii Opinion[8]). Most longline vessels oper-

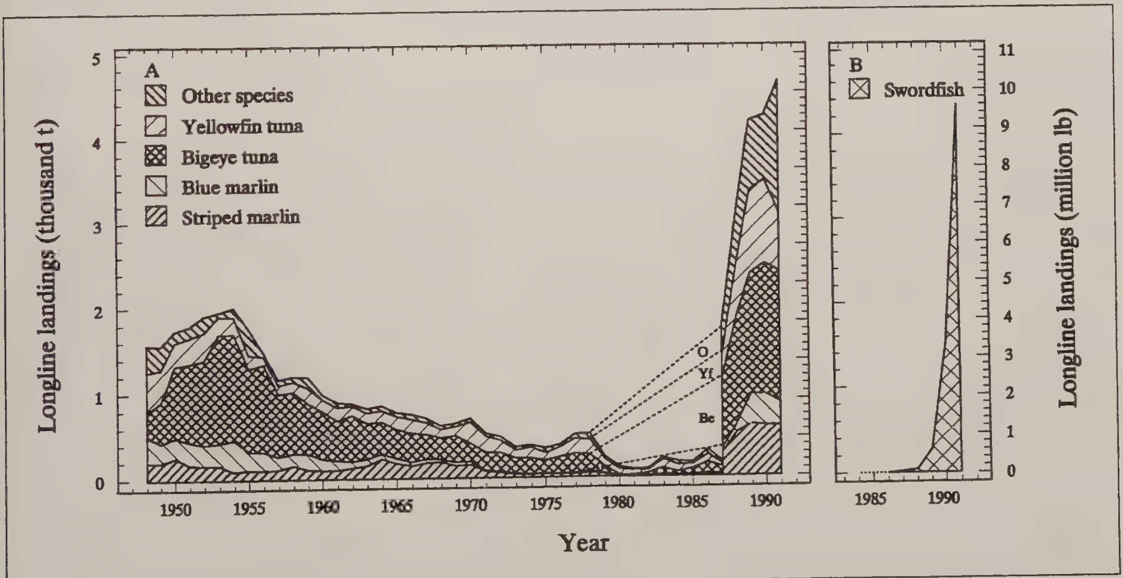

Figure 1.— Longline landings (in t and lb) in Hawaii from 1948–91, including A) component species except broadbill swordfish and B) broadbill swordfish. Total landings are the sum of stacked components. Dashed lines show corrected 1979–86 estimates for total landings, other species (O), yellowfin tuna (Yf), and bigeye tuna (Be). Sources: 1948–86, HDAR data; 1987– 91, NMFS estimates.

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[7] R. A. Dollar. 1992. Annual report of the 1991 western Pacific longline fishery. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Honolulu Lab., Southwest Fish. Sci. Cent. Admin. Rep. H-92-11, 26 p.

[8] Hawaii Opinion, Inc. 1984. A cost earnings study of the longline and handline fishing fleets in Hawaii, a summary of the survey. Prepared for NMFS, 2570 Dole St., Honolulu, HI 96822–2396, contract number 81-ABC-00267, 113 p.

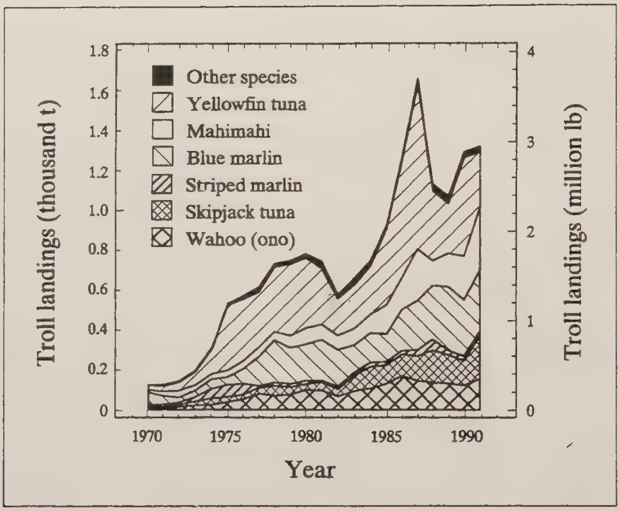

Figure 2.— Troll landings in metric tons (t) and pounds (lb) in Hawaii from 1970–91. Total landings are the sum of stacked components. Source: HDAR data.

ating through 1982 were veterans of the 1940's and 1950's. Low profitability probably contributed to the lack of investment in new vessels.

Local sale of fresh fish, mostly for raw consumption, provided a limited market that was easy to saturate, driving down the price (Otsu, 1954). The Hawaii fresh-fish market was the only outlet, because mainland U.S. consumers did not accept tuna as a fresh product. The Japan "sashimi" market was distant and exacted hard-to-meet product standards. Prices offered by tuna canneries were too low to provide adequate profits.

Although the number of vessels declined, the amount of fishing gear deployed in an average trip nearly doubled between the 1950's (Shomura, 1959) and the early 1980's (Hawaii Opinion[8]). The number of hooks per basket, and consequently the length of main line between float lines, also increased, resulting in a deeper gear configuration. A similar shift in gear configuration characterized the distant-water longline fleets of Japan and Korea (Suzuki et al., 1977; Yang and Gong, 1988).

The number of vessels participating in the Hawaii longline fishery over the years is difficult to document because many vessels fished part-time while participating in other Hawaii fisheries. June (1950) identified 49 vessels as primarily longliners (30 in Honolulu), whereas Hawaii Division of Aquatic Resources (HDAR) records indicate 76 registered longline vessels in 1950. Yoshida (1974) states that participation declined from 42 vessels in 1952 to 31 in 1964, and to 20 in 1970. Yuen[9] reported that the longline fleet in Honolulu numbered 15 in 1977, and by 1983 HDAR records showed only 13 registered longline vessels (10 in Honolulu).

The decline in vessels corresponded with the declining trend in longline landings reported to HDAR between 1954 and 1982 (Fig. 1A). However, visual inspection of the Honolulu fleet in 1983 found 37 vessels carrying longline gear (Honda[10]) as opposed t 10 registered with HDAR. Incomplete reporting to HDAR prompted the establishment of a NMFS market sampling program in late 1986 (Pooley, 1993b) and a Federal longline logbook program (Dollar and Yoshimoto[6]) was instituted by the WPRFMC in 1990 t collect more detailed data. A compari-

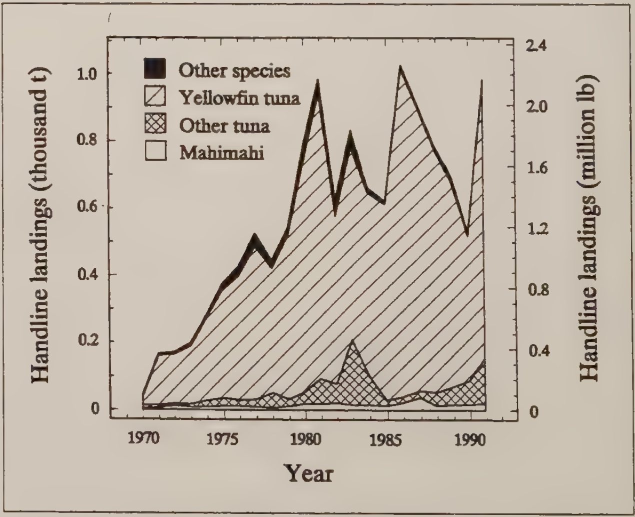

Figure 3.— Handline landings in metric tons (t) and pounds (lb) in Hawaii from 1970 to 1991. Total landings are the sum of stacked components. Source: HDAR data.

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[9] H. S. H. Yuen. 1977. Overview of fisheries fo the billfishes in Hawaii. U.S. Dep. Commer. NOAA, Natl. Mar. Fish. Serv., Southwest Fish Cent., Honolulu Lab., Southwest Fish. Cent Admin Rep. H-77-19H, 14 p.

[10] V.A. Honda. 1985. An updated description o the Hawaiian tuna longline fishery. NMFS, 30 Ala Moana Blvd., Honolulu, HI 96850–4982 unpubl. manuscri.

son between NMFS estimates of longline landings at wholesale markets and landings reported to HDAR in 1987 showed that less than 20% of longline landings were reported (Ito[2]).

The best available estimates of Hawaii longline landings over time (Fig. 1A) are based on three data sources and a correction to account for underreporting (Pooley, 1993b). HDAR longline data are believed to be relatively complete through 1978 (Pooley, 1993b). NMFS estimates based on market sampling and logbooks (Ito[2]; Pooley, 1993b) are used for 1987–91 (Fig. 1A and 1B). Estimates for 1979–86 (dashed lines, Fig. 1A) are interpolated values between HDAR reported landings in 1978 and NMFS estimates for 1987 (Pooley, 1993b). In contrast, HDAR troll (Fig. 2) and handline (Fig. 3) landings reported to HDAR through 1991 are very similar to NMFS estimates (Pooley, 1993b), and HDAR troll and handline data are used in this paper without correction. The corrected longline data indicate that the nadir of the longline fishery occured in 1975 (not 1982, Fig. 1A).

### Revitalization and Expansion

The longline fishery expanded rapidly in the late 1980's to become the largest fishery in the state. The revitalization was due to the development of the local markets and export markets for fresh tuna on the U.S. mainland and in Japan (Kawamoto et al.[11]) and the introduction of new swordfish fishing methods in the late 1980's (Dollar[7]). Participation in the Hawaii longline fishery approximately doubled from 37 vessels in 1987 to 75 in 1989 (Ito[2]) and doubled again to 156 (vessels with permits) by the end of 1991 (Dollar and Yoshimoto[6]). Permits were required by the Federal moratorium on new entrants established in 1991. Only 140 of the vessels with permits were active in 1991. In 1988 landings data first exceeded the record set in 1954 (Fig. 1A) and by 1991 landings reached 9,000 t (20 million lb), including 4,400 t (9.6 million lb) of swordfish (Fig. 1B).

New entrants in the longline fishery were mostly steel-hulled vessels up to 33 m (107 ft) in length, and the majority of these vessels and their operators were former participants in U.S. east coast tuna and swordfish fisheries (Dollar[7]). The present fleet uses modern electronics (Radar, Loran, Global Positioning System (GPS)) to navigate, and uses radio beacons, strobe lights, and radar reflectors to mark the gear. Some vessels obtain sea-surface temperature maps by radio-facsimile (FAX) and most have electronic thermometers for use in finding fish associated with temperature fronts.

Changes in fishing methods and greater amounts of fishing gear characterized the expansion of the longline fleet. In 1988 most vessels still used basket-type, rope longline gear, but they deployed over 3 times as much gear on an average trip as vessels in 1982 (Hawaii Opinion[8], Kawamoto et al.[11]). A few vessels used "bin" gear in which the rope mainline is continuous, rather than composed of baskets, and these vessels deployed similar amounts of gear as those using basket gear (Kawamoto et al.[11]). Continuous nylon monofilament main lines stored on spools and used with snap-on monofilament branch lines were first used in 1985, and by the end of 1988, 29% of the fleet used this new system (Kawamoto et al.[11]). Monofilament gear was popular among new entrants to the Hawaii fishery and became the most prevalent gear type in the fleet. Longliners using monofilament gear tended to deploy over four times as much gear per trip in 1988 (Kawamoto et al.[11]) as was typical of the fleet in 1982 (Hawaii Opinion[8]).

Monofilament longline gear is more flexible in configuration and can be used to target various depths more easily than basket gear because the amount of main line, the number of branch lines, and the sag between floats are adjustable. This flexibility was demonstrated by the switch from traditional deep daytime fishing for bigeye tuna to shallow nighttime fishing, targeting broadbill swordfish in the 1990's (Ito[2]). Both daytime and nighttime methods are still practiced using the same monofilament longline system. In targeting bigeye tuna 12–25 hooks are deployed between floats with lots of sag to reach as deep as 400 m (Boggs, 1992), whereas in targeting swordfish only a few hooks are deployed between floats and the line is kept relatively taut so that it stays in the upper 30–90 m of water. Night fishing employs luminescent "light sticks" which attract broadbill swordfish and bigeye tuna or their prey (Berkley et al., 1981). Large imported squid, *Illex* sp., are used for bait.

A special "line thrower" is required to put sag into a monofilament longline as it is deployed (Kawamoto et al.[11]; Boggs, 1992) so that it can fish deeply for bigeye tuna. Many new entrants to the fishery in 1989–91 did not invest in line throwers. These vessels fished shallow even when targeting tuna (daytime fishing) and probably contributed to the increase in the relative proportions of yellowfin tuna, blue marlin, and other shallow-swimming species caught by longliners in recent years (Fig. 1A). The increasing longline catch of these species was cause for concern by the small-vessel troll and handline fisheries that target them (Boggs[3]).

The fishing grounds of the Hawaii longline fishery expanded in the 1980's and 1990's. Hawaii fishermen interviewed in 1982 reported that they had to fish farther away from port in order to make good catches (Hawaii Opinion[8]). In 1986 Hawaii longliners began exploring fishing grounds up to 800 n.mi. from the main Hawaiian Islands, and distant-water fishing is becoming more common in the 1990's. Logbook data from the first quarter of 1991 indicate that over half of longline sets were more than 50 n.mi. away from the main Hawaiian Islands, and <2% of sets were made outside the EEZ (NMFS[12]).

Conflicts with other fisheries and interactions with protected species led to the exclusion of the longline fishery from nearshore waters in the 1990's. In early 1991 longline fishing was prohibited within a radius of 50 n.mi. off the NWHI (Dollar[7]) to prevent interactions between endangered Hawaiian monk seals, *Monachus schauinslandi*, and surface-fishing longliners that targeted aggregations of swordfish near those islands. In 1989 an informal agreement was negotiated between small-vessel fishermen and longline fishermen whereby longliners would keep >20 n.mi. from the coasts of the main Hawaiian Islands and >10 n.mi. from fish aggregating devices (FAD's). Some vessels, especially subsequent entrants to the fishery, did not comply with the agreement. To mitigate conflicts between longliners and small-vessel troll and handline fishermen, the WPRFMC in mid-1991 established a buffer zone prohibiting longline fishing within a radius of 75 n.mi. off the coasts of Kauai and Oahu, or within a radius of 50 n.mi. off the coasts of Maui, Molokai, Lanai, Kahoolawe, and Hawaii (Dollar and Yoshimoto[6]).

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[11] K. E. Kawamoto, R. Y. Ito, R. P. Clarke, and A. E. Chun. 1989. Status of the tuna longline fishery in Hawaii, 1987–88. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-89-10, 34 p.

[12] NMFS Honolulu Laboratory, 2570 Dole St., Honolulu HI 96822-2396, unpubl. longline logbook data.

## The Troll Fishery

Troll and handline fisheries in Hawaii have not been studied as extensively as the longline fishery. Trolling involves towing lures or baited hooks behind a moving vessel, whereas handlining involves dangling baited hooks from a stationary or drifting vessel. The evolution and operation of the Hawaii troll fishery are poorly documented. Trolling with lures for pelagic species was a traditional Polynesian fishing method, and Hawaii has since been the site of important innovations in big-game troll fishing techniques (Rizzuto, 1983).

The troll fishery has several components: 1) a recreational-subsistence sector which is poorly differentiated from a part-time commercial sector, 2) a charter sector which is recreational for its patrons but commercial for the operators who sell the catch, 3) a part-time commercial sector, and 4) a full-time commercial sector. Most troll vessels are small (5–8 m, 15–25 ft in length), although charter boats range up to 18 m (59 ft). In the mid-1980's large (20–26 m, 65–85 ft) troll vessels transiting the Hawaii EEZ to fish for albacore, *Thunnus alalunga*, in the North Pacific participated briefly in the Hawaii troll fishery, and vessels from the lobster and bottomfish fisheries also participate intermittently in the Hawaii troll fishery. Troll fishing is conducted throughout the Hawaiian islands, generally within 20 n.mi. of shore.

Commercial catch reports to HDAR do not distinguish between different types of troll fishing (i.e., part-time, charter); only fishermen who sell their catch are required to file reports. Reported annual commercial troll catches were <200 t (0.4 million lb) until 1974 (Fig. 2). During 1975–84 catches ranged between 540–790 t (1.2–1.7 million lb) per year, and then the catch rose to a record peak of almost 1,700 t in 1987. Annual catches declined after 1987 but remained >1,000 t (2.2 million lb) through 1991 (Fig. 2).

The troll fishery catches more mahimahi and wahoo, *Acanthocybium solandri*, than all the other Hawaii pelagic fisheries, about half the blue marlin, and about 20% of the yellowfin tuna landed. Yellowfin tuna composed almost half the commercial troll catch from 1975 to 1980, after which its proportion in the catch declined. The proportion of mahimahi and skipjack tuna in the troll catch increased through the 1980's and 1990's. The charter sector of the troll fishery targets blue marlin, and this species accounted for 54% and 39% of estimated charter catches in 1976 (Cooper and Adams[13]) and 1982 (Samples et al.[14]), respectively. In contrast, 87% of full-time commercial troll catches were yellowfin tuna (Cooper and Adams[13]). Changes in the relative size of the different commercial sectors (i.e., charter, part-time) may influence the species composition of the total reported catch (Fig. 2).

Charter vessels in the troll fishery numbered 102 and 119 in 1976 and 1982, respectively (Cooper and Adams[13]; Samples et al.[14]), compared to an estimated 160 full-time commercial, and 1,544 part-time and recreational-subsistence trollers (combined) in 1976 (Cooper and Adams[13]). Proportions of the total troll catch by these sectors in 1976 were 21% charter, 44% part-time commercial and recreational-subsistence (combined), and 35% full-time commercial. About 70% of the charter catch and 60% of the part-time commercial and recreational-subsistence catch was sold (Cooper and Adams[13]). Growth of the troll fishery makes it unlikely that these proportions represent the current situation but the charter fishery is believed to have grown with the expansion of tourism, and the recreational-subsistence fishery remains important (Pooley, 1993a).

## The Handline Fishery

There are several types of pelagic handline fishing in Hawaii today. Day-handline fishing is a revitalization of an ancient Hawaiian method called "palu-ahi" for the use of "palu" (chum) to attract and hook ahi (yellowfin tuna). Palu-ahi fishing is also called "drop stone" fishing. A baited hook on the end of the handline is laid against a stone and the line wound around it. Additional pieces of chum are also wound into the bundle which is then tied in a slip knot (Rizzuto, 1983). The bundle is lowered to the preferred depth (commonly 20–30 m). Then the line is jerked to untie the knot so that the baited hook and chum are released.

Night-handline fishing is called "ika-shibi" from the Japanese names for squid (ika) and tuna (shibi). The ika-shibi fishery is an outgrowth of a squid fishery that probably began in the 1920's and did not target tuna until after World War II (Yuen, 1979). Ika-shibi fishermen attract squid to the fishing vessel with a light and catch the squid on jigs or with a gaff. The squid are then used as bait. Ika-shibi or palu-ahi were not distinguished as separate fishing methods in HDAR statistics prior to 1982. Subsequently (1982–91) only a fraction of handline landings were reported as palu-ahi or ika-shibi, and so the handline catch statistics have been combined for this report (Fig. 3).

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[13] J. C. Cooper and M. F. G. Adams. 1978. Preliminary estimates of catch, sales, and revenue of game fish for the fishing conservation zone around the main Hawaiian Islands, by types of troll and longline vessels and by species. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. 24H, 10 p.

[14] K. C. Samples, J. N. Kusakabe, and J. T. Sproul. 1984. A description and economic appraisal of charter boat fishing in Hawaii. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-84-6C, 130 p.

All handline catches were sold on the Island of Hawaii where the fishery was primarily located until 1971 when the rising price for tuna and reduced shipping costs made air shipment to Honolulu economically feasible. The increasing market for fresh fish boosted the development of Hawaii's fisheries in the mid-1970's (Pooley, 1993a). Annual commercial handline landings reported to HDAR increased from 45 t to almost 1,000 t between 1970 and 1981. Since 1981 commercial handline landings have ranged between 500 and 1,000 t (1.1–2.2 million pounds) with major peaks in 1981, 1983, 1986, and 1991 (Fig. 3). The magnitude of the recreational-subsistence sector of the handline fishery is unquantified, but important (Pooley, 1993a).

The composition of the handline catch is almost exclusively tuna; yellowfin tuna is the predominant species (Fig. 3). Mahimahi and other nontuna species make up less than 10% of the catch. Bigeye tuna are an important component of the handline catch (Yuen, 1979) that is not reflected in HDAR statistics. The ika-shibi catch of bigeye tuna ranged from 63 to 120 t (139–265 thousand lb) in 1973–75 (Yuen, 1979), but HDAR records indicate <23 t of tuna other than yellowfin landed by all handline fishing gears in 1973–75 (Fig. 3). This may represent a lack of reporting, but it is also likely that handline fishermen are lumping both bigeye and yellowfin catches as ahi in their catch reports since these species have the same Hawaiian name.

Most handline vessels are 6–9 m in length and are often crewed by 1–2 persons. Surveys by Yuen (1979) and Ikehara[15] indicate that the ika-shibi fishery grew from 30–40 boats in 1976 to at least 230 boats by 1980. In recent years some of the smaller longline vessels and larger commercial troll vessels have also done some handline fishing.

Day-handline fishing was concentrated around the Island of Hawaii and ika-shibi fishing was concentrated off the Hilo coast of Hawaii in the mid-1980's. Traditionally, handline fishing was conducted within a few km of the coast at locations called "ahi koas" where yellowfin and bigeye tuna were especially available. The State (HDAR) encouraged expansion into new areas in the late 1980's. Handline fishing techniques have spread and are now practiced on Kauai and Maui. Some of the largest handline vessels have extended their range to fish around seamounts and weather buoys 100–200 n.mi. from the coast. This new expansion of the fishery may have contributed substantially to the peak in catch reported in 1991, which followed four years of continuous decline (1987–90, Fig. 3). Some fishermen feel that there may soon be too many participants in the handline fishery, and the WPRFMC has been asked to institute a control date for this fishery in anticipation of possible limited-entry management.

The increasing cost of insurance has been a problem for small-vessel commercial fishermen. Many operators could not afford to keep up with rising insurance costs in the late 1980's and some, who weren't willing to risk their assets, stopped fishing. Another economic problem for the commercial troll and handline fisheries is a condition called burnt tuna syndrome (BTS) which discolors and gives a bad taste to sashimi as well as reduces its shelf life (Nakamura et al., 1987). BTS is prevalent in troll and handline-caught fish over 35 kg and uncommon in longline-caught fish. Proper handling can ameliorate BTS (Nakamura et al., 1987) and research is under way to find means to prevent it (Watson et al., 1988).

## Abundance and Availability

### Background

The primary concern in Hawaii's pelagic fisheries today is whether fishing effort should be limited to protect the local abundance or availability of fish (Pooley, 1990; Boggs[3], In press; Skillman et al., 1993). Increased catches by Hawaii's pelagic fisheries over the last two decades could hypothetically have reduced the abundance of local stocks, if such stocks exist. It is more likely that Hawaii's fisheries exploit locally available fractions of Pacific-wide stocks (Wetherall and Yong[16]; Skillman and Kamer[4]; Boggs, In press). In the latter case immigration may limit yields and excessive fishing effort might result in reduced CPUE (Sathiendrakumar and Tisdell, 1987; Boggs[3], In press). In either case, excessive local fishing pressure should be evidenced by corresponding declines in local CPUE.

Several studies suggest that local fishing pressure can reduce local CPUE for wide-ranging pelagic species (Wetherall and Yong[16], Squire and Au, 1990; Boggs[3], In press; Skillman and Kamer[4]). Many of these studies also found that the relative abundance (CPUE) of fish over a wider geographic area could statistically account for much of the variation in local CPUE. Relative abundance estimated as CPUE is confounded with catchability, so that widespread environmental effects on catchability, as well as true changes in stock-wide abundance, could explain the statistical relationships between Pacific-wide CPUE and local CPUE.

The following examination of Hawaii CPUE time series extending from the early years of each fishery to the present was undertaken to show whether or not the expansion of Hawaii's pelagic fisheries over the last two decades, 1970–91, corresponded with declines in local CPUE. Major declines in local CPUE were often found to predate local fisheries expansion and corresponded with declines in the CPUE of more widespread fisheries. Over the last few decades the time series indicated much interannual variation and little net change in CPUE.

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[15] W. N. Ikehara. 1981. A survey of the ika-shibi fishery in the State of Hawaii, 1980. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-82-4C, 12 p.

[16] J. A. Wetherall and M. Y. Y. Yong. 1983. An analysis of some factors affecting the abundance of blue marlin in Hawaiian waters. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-83-16, 33 p.

### Calculation of Hawaii CPUE

Longline CPUE was calculated from a combination of data sources including published literature, HDAR data summaries, and NMFS market sample estimates. Troll and handline CPUE was calculated solely from HDAR data summaries because these data identify troll and handline gears (NMFS estimates do not). HDAR summaries do not differ substantially (in total) from NMFS estimates for combined troll and handline (Pooley, 1993b). All available summary statistics (HDAR and NMFS) were used in the present study, but no new analyses of raw data were conducted.

To calculate CPUE in the early longline fishery (e.g., Fig. 4A), Hawaii longline data on two size-classes of vessels for 1948–56 (Shomura, 1959) were combined, and catch was converted from number of fish to weight. The results were similar to 1948–52 CPUE data published by Otsu (1954). The CPUE based on combined data differed little from the data for large vessels (Shomura, 1959), and although vessel size is important, it was ignored in the present study because data summaries by vessel size for subsequent years were not available.

Longline data summaries for 1959–89 and NMFS market sample longline estimates for 1987–89 (Ito[2]; Pooley, 1993b) were used to calculate longline CPUE for later years (e.g., Fig. 4A). HDAR longline data after 1978 are believed to represent only a fraction (ca. <20% Fig. 1A) of the fishery, but complete coverage is not required to calculate a representative CPUE index. No other data were available for 1979–86.

Two longline CPUE indices for 1987–89 were calculated, one from HDAR data, and another from NMFS estimates (e.g., Fig. 4A). The HDAR series from 1979 through 1989 best indicates the longline CPUE trend for those years, whereas the 1987–89 NMFS data best indicate recent CPUE for comparison with the earlier years 1947–78 (e.g., Fig. 4A). Longline CPUE was not calculated for 1990–91 because in these years a fraction of the longline fishery changed fishing methods to target broadbill swordfish, and additional work is needed to categorize the subset of the longline trips in 1990–91 that targeted tuna. The Hawaii swordfish fishery has developed too recently (Fig. 1B) for any trend in CPUE to be indicative of availability.

HDAR data summaries for the troll and handline fisheries from 1970 to 1991 were used to calculate CPUE time series for these fisheries (e.g., Fig. 4B). Prior data are not very important because the troll and handline fisheries were so small before 1970.

CPUE was calculated as the total annual longline, troll, or handline catch (by weight) of a species divided by total annual effort. Effort was estimated either as the annual number of fishing trips (troll and handline fisheries) or the annual number of hooks (longline fishery). Longline hook totals were calculated from the number of trips multiplied by estimates of hooks per trip (Boggs and Hawn[17]). Changes in the amount of gear deployed per trip obtained from descriptions of the fishery (June, 1950; Otsu, 1954; Shomura, 1959; Hida, 1966; Yoshida, 1974; Hawaii Opinion[8]; Kawamoto et al.[11]; Ito[2]) were used to estimate and interpolate the typical quantity of hooks per trip from 1947–89 (Boggs and Hawn[17]). Corrections for changes in efficiency with fishing depth are being developed (Boggs, 1992; Boggs and Hawn[17]) but are not used here.

The NMFS market sampling program counted fishing trips as each occasion that a vessel landed and sold its catch. HDAR data summaries included each unique date of landing for each unique license number in the records as a trip if any pelagic species were caught. Trip counts from both NMFS and HDAR data did not include trips with no catch of any pelagic species (prior to 1992). Such trips were seldom reported. For any given species the count of trips did include trips that did not catch that species but caught another pelagic species.

The lack of data on the number of trips that caught no pelagic species may have caused errors in the effort estimates, but the CPUE time series based on those data may still be indicative of relative changes in availability. The number of zero-catch trips should have been negatively correlated with catch per successful trip (CPUE) since both were dependent on fish availability. Thus, the CPUE time series should still reflect real trends, especially if zero-catch trips represented a modest fraction of total effort. No bias was caused by changes in the fraction of zero-catch trips reported because none were counted. Uchida (1976) found a high correlation between Hawaii pole-and-line CPUE including zero-catch trips and CPUE excluding zero-catch trips.

The effort data for the troll and handline fisheries contained no standardization of trips as a unit of effort, and the longline effort data were standardized only to account for changes in the number of hooks per trip (Boggs and Hawn[17]). Changes in troll or handline fishing power, (number of lines, hooks, or hours, per trip, etc.) or changes in longline, troll, or handline efficiency (class of vessel, gear type, target depth, fishing strategy) may have resulted in biases in the CPUE time series, obscuring trends or giving the appearance of trends where none existed. Although much of the data presented here are decades old, the estimates of CPUE must be considered preliminary until the raw data are reanalyzed and effort standardized to account for changes in efficiency (e.g., Uchida, 1976; Suzuki, 1989).

Despite problems with the nonstandardized CPUE indices, they are the only data currently available. Nonstandardized Hawaii CPUE data for several different gear types often show a similar pattern (Skillman and Kamer[4]) or reflect a pattern similar to that of more sophisticated CPUE indices from nearby fisheries (Wetherall and Yong[16]). These examples suggest that some true information on relative availability is represented by nonstandardized CPUE indices for Hawaii's fisheries.

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[17] C. H. Boggs and D. R. Hawn. Changes in fishing power and estimates of fishing effort for the Hawaii longline fishery, 1948–91. NMFS Honolulu Laboratory, 2570 Dole St., Honolulu HI 96822–2396, unpubl. manuscr.

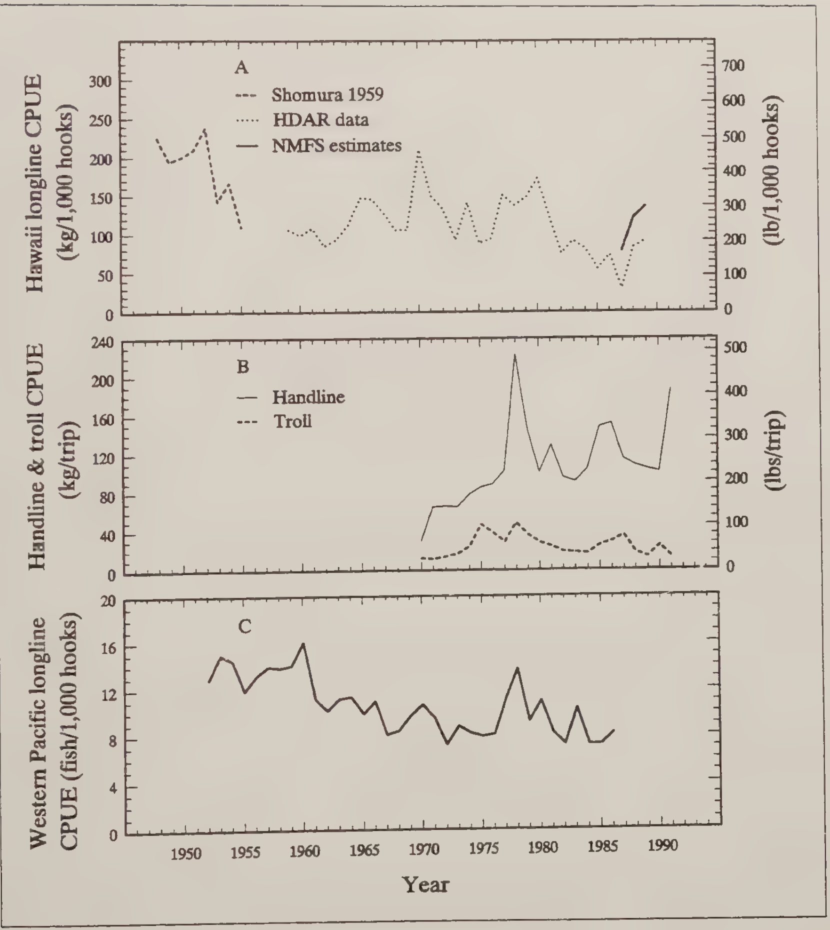

Figure 4.— Yellowfin tuna CPUE time series showing A) Hawaii longline CPUE (kg and lb per 1,000 hooks) from 1948–55 (Shomura, 1959), 1959–89 (HDAR data), and 1987–89 (NMFS estimates); B) Hawaii handline and troll CPUE (in kg and lb per trip) from 1970 to 1991 (HDAR data), and C) western Pacific longline CPUE (in no. fish per 1,000 hooks) in the Japanese fishery from 1952 to 1986 (Suzuki, In press).

### CPUE Time Series

Yellowfin tuna CPUE in the Hawaii longline fishery declined between the 1950's and the early 1960's and then ranged between 90–210 kg/1,000 hooks with no clear trend from 1959–81 (Fig. 4A). Yellowfin tuna CPUE based on HDAR longline data declined from 1980–87, recovering somewhat in 1988–89. The more accurate longline CPUE index based on NMFS estimates indicated a return to average longline CPUE in 1988–89 (Fig. 4A).

The 1980–87 decline in yellowfin tuna CPUE for the Hawaii longline fishery occurred during a period of troll (Fig. 2) and longline (Fig. 1A) fishery expansion. However, the subsequent increase in longline CPUE in 1988–89 occurred during the period of greatest longline fishery expansion, while troll and handline fishing levels remained very high. Thus low levels of Hawaii longline CPUE did not correspond consistently with periods of higher fishing pressure.

Yellowfin CPUE in the Hawaii troll and handline fisheries (Fig. 4B) increased from 1970 to 1978 and subsequently declined through 1984. After 1984 Hawaii handline and troll CPUE increased to peaks in 1986 and 1987, respectively, and then declined (Fig. 4B). These declines coincided with expansion of Hawaii's longline, troll, and handline fisheries. However, handline CPUE subsequently increased from 1884 to 1986 and troll CPUE increased from 1984 to 1987 despite continued expansion of the troll and longline fisheries. During the period of greatest expansion of the longline fishery

(1987–89) troll and handline CPUE declined (Boggs[3]). However, troll CPUE returned to a typical level in 1990 and handline CPUE reached a high level in 1991 (Fig. 4B) despite continued high levels of fishing by all three pelagic fisheries. Thus availability (CPUE) of yellowfin tuna in Hawaii did not appear to be closely related to changes in local fishing pressure.

Local availability of yellowfin tuna seemed to follow patterns in the overall abundance or catchability of the stock as indicated by CPUE in wide-ranging Japanese longline and purse seine fisheries. Standardized yellowfin tuna CPUE in the longline fishery of Japan in the western Pacific from 1952 to 1986 (Suzuki, In press) indicated a drop in CPUE between the 1950's and early 1960's, and a decline in the early 1980's (Fig. 4C) similar to that seen in Hawaii longline CPUE data (Fig. 4A). In more recent years (1983–88), Hawaii troll CPUE followed a pattern that was similar to Japanese western Pacific purse-seine CPUE (Suzuki, In press; Boggs, In press; Skillman et al., 1993). Environmental anomalies affecting catchability may contribute much of the corresponding variation seen in CPUE time series, such as the peak in yellowfin tuna CPUE that occurred in 1978 (Fig. 4A and 4B).

An initial increase in bigeye tuna CPUE in the early years of the Hawaii fishery (Fig. 5A) was explained by Shomura (1959) as the result of a change in the area fished during winter as fishermen learned to target bigeye tuna. Set depth also changed between the late 1940's and early 1950's as the practice of buoying up the middle of each basket of gear with an extra float (June, 1950) was abandoned. Deep gear has been shown to be more efficient than shallow gear in catching bigeye tuna (Hanamoto, 1976; Suzuki et al., 1977; Boggs, 1992).

Bigeye tuna CPUE in the Hawaii longline fishery (Fig. 5A) and in the wide-ranging Japanese longline fishery (Fig. 5B) (Miyabe, In press) both showed downward trends from the late 1950's through the 1960's, a distinct drop in CPUE in 1970, a stable period in the mid-1970's, record low levels in 1980–81, and a slight recovery in the mid 1980's. The correspondence between the bigeye tuna CPUE statistics for the entire Pacific and for Hawaii is remarkable, and strongly suggests that local pelagic fish availability is linked to the abundance of a widespread population. An alternative hypothesis that could apply to all of the pelagic species is that CPUE variation is due to widespread changes in catchability associated with environmental trends.

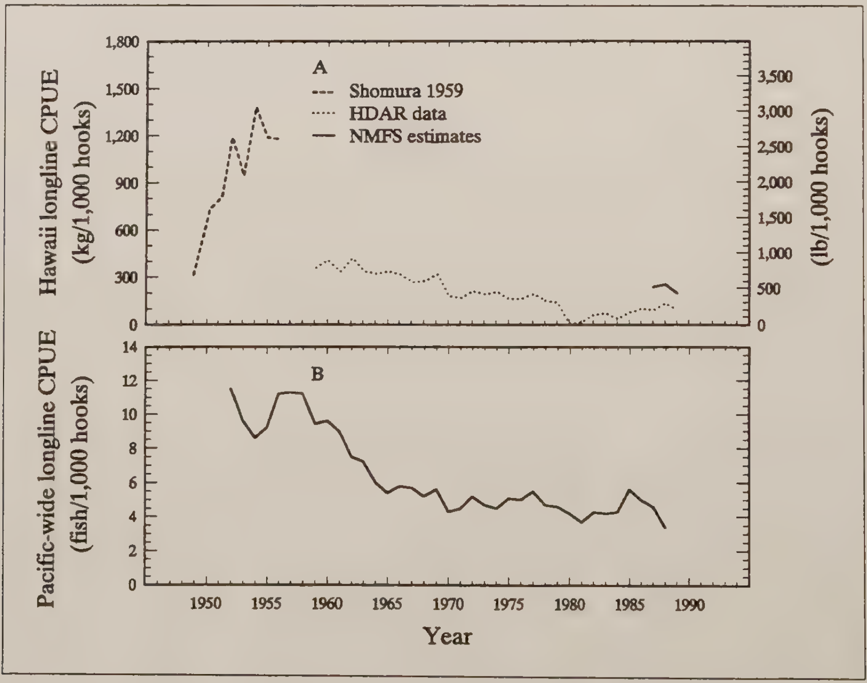

Figure 5.— Bigeye tuna CPUE time-series showing A) Hawaii longline CPUE (in kg and lb per 1,000 hooks) from 1949 to 1956 (fiscal years ending in June, Shomura, 1959), 1959–89 (HDAR data), and 1987–89 (NMFS estimates), and B) Pacific-wide longline CPUE (in no. fish per 1,000 hooks) in the Japanese fishery from 1952 to 1987 (Miyabe, In press).

For bigeye tuna, the Hawaii longline CPUE continued to recover in the late 1980's (Fig. 5A), whereas Japanese CPUE declined (Fig. 5B). The increasing trend in Hawaii bigeye tuna CPUE in the 1980's brought the CPUE index based on NMFS wholesale market sample back up to a level slightly higher than the average for 1970–78 (Fig. 5A) suggesting that local longline fishery expansion in the 1980's did not negatively affect bigeye tuna availability.

The blue marlin CPUE time series for the Hawaii longline fishery (Fig. 6A) showed peaks and minima for the same years as the Hawaii troll CPUE time series (Fig. 6B). The close correspondence between blue marlin CPUE in these two fisheries suggests that both CPUE time series reflected true changes in availability or catchability despite the limitations of the available statistics.

Blue marlin (Fig. 6A) and striped marlin (Fig. 7A) CPUE in the Hawaii longline fishery followed a pattern similar to Japanese longline CPUE data (Fig. 6C and 7B), as noted by Wetherall and Yong[16] and Skillman and Kamer[4]. This correspondence was not limited to the long-term decline in CPUE characteristic of longline fisheries in all oceans. Rather, for striped marlin both increases and decreases in CPUE in the Hawaii longline fishery (Fig. 7A) corresponded with CPUE changes in the North Pacific Japanese longline fishery (Fig. 7B).

The sharp increase in longline CPUE for blue and striped marlin in 1989 probably reflected the increased use of monofilament longline gear without

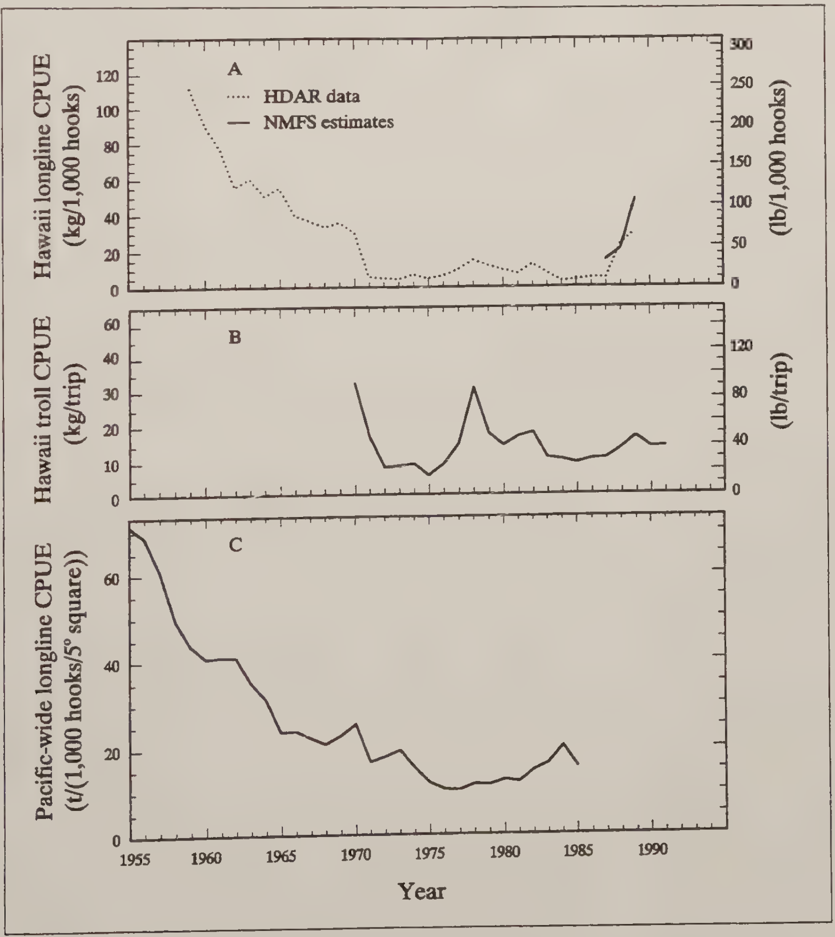

Figure 6.— Blue marlin CPUE time-series showing A) Hawaii longline CPUE (kg and lb per 1,000 hooks) from 1959 to 1989 (HDAR data), and 1987–89 (NMFS estimates), B) Hawaii troll CPUE (in kg and lb per trip) from 1970 to 1991 (HDAR data), and C) Pacific-wide longline CPUE (in t per 1,000 hooks per 5° square) in the Japanese fishery from 1955 to 1985 (Suzuki, 1989).

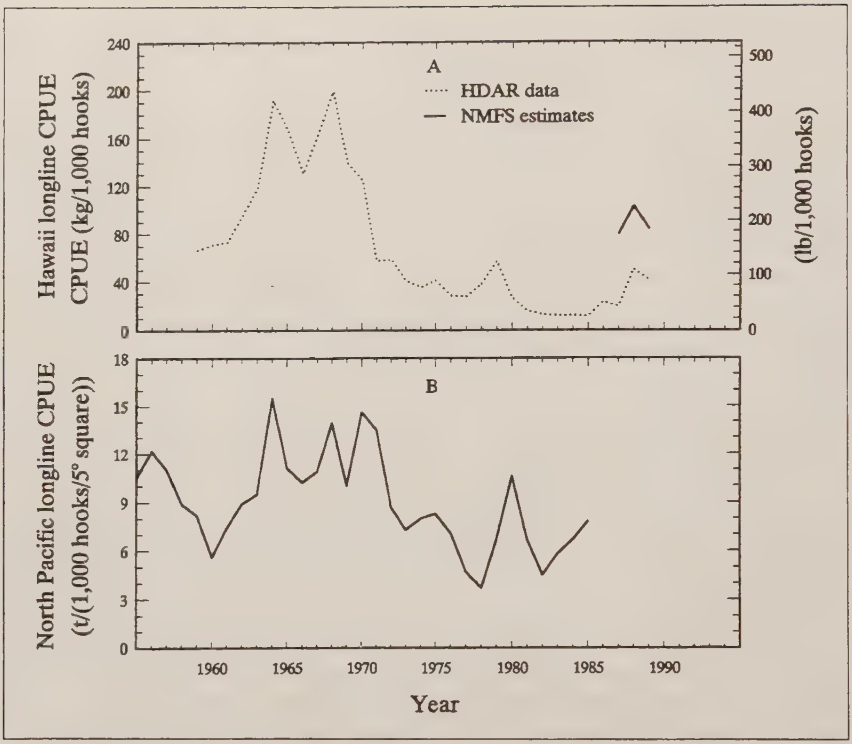

Figure 7.— Striped marlin CPUE time series showing A) Hawaii longline CPUE (in kg and lb per 1,000 hooks) from 1959 to 1989 (HDAR data), and 1987–89 (NMFS estimates), and B) North Pacific longline CPUE (in t per 1,000 hooks per 5° square) in the Japanese fishery from 1955 to 1985 (Suzuki, 1989).

line-throwers, which resulted in shallower sets and increased the efficiency of the gear for marlin (Suzuki, 1989; Boggs, 1992). Blue marlin CPUE in the troll fishery appears to be at a normal level and relatively stable (Fig. 6B) despite the expansion of Hawaii's pelagic fisheries.

Mahimahi CPUE in the Hawaii longline fishery (Fig. 8A) reached a peak in 1972 and a minimum in 1988 that were mirrored in the Hawaii troll and handline CPUE data (Fig. 8B). Troll and handline CPUE data corresponded with each other very closely. Mahimahi CPUE appears to be increasing in both the troll and handline fisheries.

## Outlook for the Pelagic Fisheries

The absence of clear declining trends in local CPUE associated with local fishery expansion, combined with distinctly seasonal variations in CPUE (Shomura, 1959; Yoshida, 1974; Skillman and Kamer[4]), suggests that pelagic fish availability in Hawaii was most strongly affected by factors other than local fishing pressure. Anomalies in whatever factors control seasonal availability could also be the major source of interannual variation in CPUE. Research leading to an ability to forecast changes in pelagic fish availability could ameliorate fishermen's concerns that local fishing pressure has decreased fish availability. Development of new methods to locate or predict productive fishing areas could increase the yield and efficiency of Hawaii's pelagic fisheries. However, greatly increased fishing efficiency and yield might then have some negative impact on local fish availability.

Decreases in fish availability caused by local fishing pressure may have been obscured by biases such as increased fishing power, expansion into more productive fishing grounds, economic influences on fishing operations, and environmental influences on local abundance and catchability. Further analysis of catch and effort data as well as an improved data collection system are needed to attempt to account for such biases. However, the parsimonious explanation of the available data is that locally exploited stocks have not yet been impacted by the expansion of Hawaii's pelagic fisheries.

Long-term declines in the overall apparent abundance of many pelagic species occurred several decades ago (Figs. 4C, 5C, and 6C), before the latest (1970–91) expansion of Hawaii's pelagic fisheries. Pacific-wide declines in CPUE do seem to affect Hawaii's fisheries, and could reflect full exploitation or even overexploitation of the stocks. However, reduction of local

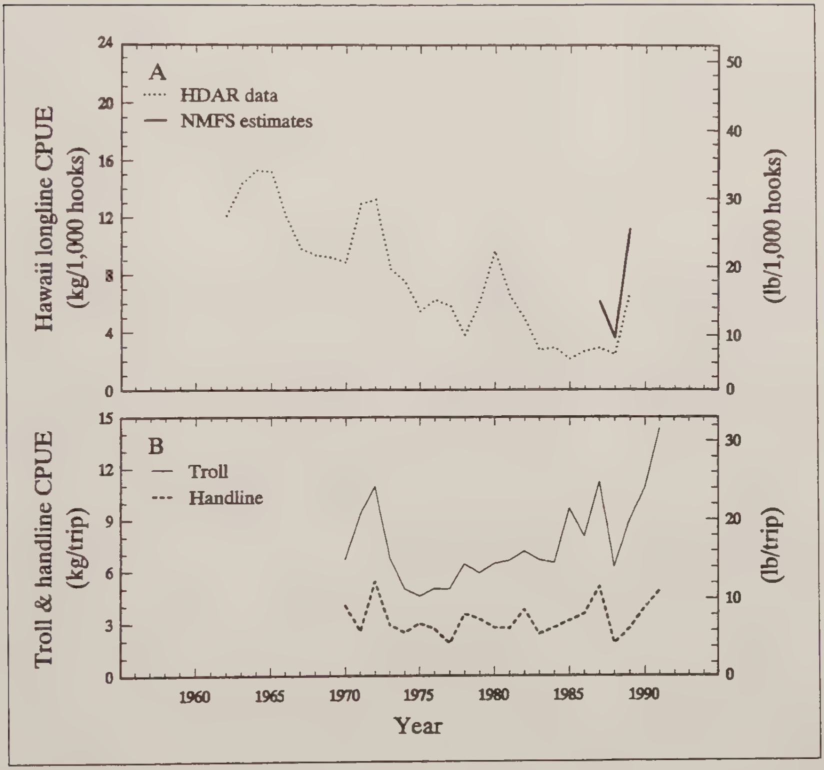

Figure 8.— Mahimahi CPUE time series showing (A) Hawaii longline CPUE (kg and lb per 1,000 hooks) from 1962 to 1989 (HDAR data), and 1987–89 (NMFS estimates), and (B) Hawaii troll and handline CPUE (in kg and lb per trip) from 1970 to 1991 (HDAR data).

fishing effort from current levels would not substantially affect stock-wide abundance because of the relatively small scale of Hawaii's pelagic fisheries. An exception might be the nighttime longline fishery for broadbill swordfish, which has been operating for too short a time to evaluate. However, with annual landings of 4,400 t and continued growth, the Hawaii swordfish fishery may be expected to contribute significantly to total fishing mortality on the stock. Historically, maximum total Pacific yields of swordfish have been on the order of 20,000 t per year (Bartoo and Coan, 1989).

If fishery managers can prevent physical conflicts between the longline and small-vessel troll and handline fisheries in Hawaii (Pooley, 1990; Skillman et al., 1993), and if adequate markets continue to support the profitable operation of all fishery sectors, then Hawaii's pelagic fisheries should continue to expand. No strong evidence suggests that the local availability of fish is a factor limiting further expansion. However, this optimistic assessment is based on statistics and analyses that may be inadequate; therefore, better fishery monitoring systems are needed.

## Acknowledgments

We thank Reggie Kokubun of HDAR for producing the data summaries for Hawaii's longline, troll, and handline fisheries for 1970–91. This paper is dedicated to Justin Rutka, longtime member of the WPRFMC's Pelagic Fishery Management Plan Team, in response to his unswerving quest to examine local pelagic CPUE time series.

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# The Development and Decline of Hawaii's Skipjack Tuna Fishery

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*ABSTRACT—The pole-and-line fishery for skipjack tuna,* Katsuwonus pelamis, *was the largest commercial fishery in Hawaii until its decline in the 1970's and 1980's. The development and decline of the fishery were strongly affected by fish availability and marketing. A sustained drop in the availability of large fish in the mid-1970's appears to have been due in part to a sustained environmental change. Availability of large fish subsequently increased, but the fishery continued its decline owing to low profitability and lack of markets. The tuna cannery in Honolulu that fostered the fishery's expansion in the 1930's closed in 1984. Unless efforts to increase the market for skipjack tuna become effective, landings will probably remain at current levels of about 1,000 metric tons per year. The existing pole-and-line fleet may continue to decline with age, and the local market may eventually be supplied by other fishing methods (e.g., trolling), by new vessels, or by imports.*

## Introduction

Historically, the pole-and-line, live-bait fishery for skipjack tuna, *Katsuwonus pelamis*, was the largest commercial fishery in Hawaii. Annual pole-and-line landings of skipjack tuna exceeded 2,500 metric tons (t) or 5.5 million lb from 1937 to 1973 (June, 1951; Yamashita, 1958; Uchida, 1976; Skillman, 1987; Kikkawa[1]), except during World War II (1941–45). The record production of 7,400 t (16.3 million lb) of all species landed in 1965 by the pole-and-line fishery was unsurpassed until 1991, when the Hawaii longline fishery landed 8,000 t (all species combined). Even so, at its largest, the Hawaii skipjack tuna catch was small compared with the total Pacific catch of this species (ca. 870,000 t in 1990; IATTC, 1992; Hampton, In press).

The Hawaii skipjack tuna fishery originally supplied only the local market for fresh and dried tuna. The fishery expanded in the 1900's because the ready availability of skipjack tuna was sufficient to support a cannery which provided access to outside markets. A sustained drop in the catch per unit effort (CPUE) of large (>6.8 kg, >15 lb) skipjack tuna began in 1974. The decrease in CPUE was related to environmental changes affecting local fish availability (Mendelssohn[2]; Boggs, 1988). Combined with increased fishing costs, market competition from other tuna products, and the 1984 closure of the Hawaiian Tuna Packers, Ltd. cannery in Honolulu, these factors caused a major decline in Hawaii's skipjack tuna fishery during the late 1970's and 1980's (Boggs and Pooley, 1987; Hudgins and Pooley, 1987). The fishery has not recovered.

Expanding fisheries for skipjack tuna throughout the Pacific (Forsbergh, 1980; IATTC, 1992; Hampton, In press) do not appear to have caused the decline in Hawaii's fishery (Boggs and Pooley, 1987; Kearney, 1987; Sibert, 1987), although further analyses may reveal negative impacts. Skipjack tuna are relatively impervious to overfishing (Boggs and Pooley, 1987; Hampton, In press) due to widespread distribution and reproduction, rapid growth, early maturity (Matsumoto et al., 1984), and frequent spawning (Hunter et al., 1986). Unlike populations of larger tuna species (Miyabe, In press; Suzuki, In press) and marlins (Suzuki, 1989), skipjack tuna appear to be underexploited (Kleiber et al., 1983; Hampton, In press). The absence of regulation in Hawaii's skipjack tuna fishery contrasts with the management of Hawaii's fisheries for other tunas and billfish (Boggs and Ito, 1993), and is justified by the apparent underexploitation of the stock and the declining size of the local fishery.

This review describes the Hawaii skipjack tuna fishery, its development through the 1970's, and subsequent decline. Research on factors contributing to the decline are summarized and the fishery community's attempts at revitalization are described.

## Description and Historical Development

In Hawaii, skipjack tuna, commonly called by its Hawaiian name "aku," is mostly caught by pole-and-line fishing (e.g., >99% through 1974, 72% in 1990). This method uses live bait thrown from a fishing vessel to stimulate a surface school into a feeding frenzy. Fishing is then conducted frantically to take advantage of the limited time the school remains near the boat. The pole and line are of equal length (ca. 3 m) and are used with a barbless hook with feather skirts which is slapped against the water until a fish strikes. Then the fish is yanked into the vessel in one motion. The fish unhooks when the line is slacked so that the process can be repeated.

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[1] Bert S. Kikkawa. An update of the skipjack tuna, *Katsuwonus pelamis*, baitboat fishery in Hawaii, 1971–83. Honolulu Lab., Southwest Fish. Sci. Cent., NMFS, 2570 Dole St., Honolulu, HI 96822–2396, unpubl. manuscr.

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The bait most often used is the anchovy *Encrasicholina purpureas*, commonly called by its Hawaiian name "nehu." Each fishing vessel seines for bait in bays, harbors, and other sheltered waters, and the bait is not "hardened" for long-term transport or for use more than a few days after capture. The fishery is limited to areas close to the eight main Hawaiian Islands. Skipjack tuna are located by searching for bird flocks associated with surface schools. Fishing trips seldom last longer than a day, and most vessels return to port each night.

The basic pole-and-line method in use today was practiced in the 1800's largely by native Hawaiians using canoes (June, 1951). In 1900 the fishery was relatively small, with total landings of 190 t (0.4 million lb, Fig. 1) sold in the fresh market (Yamashita, 1958). Around the turn of the century Japanese immigrants began introducing small (ca. 6 m) shallow-draft wooden sampans with built-in bait wells, followed by motor powered vessels starting in 1907. In the 1930's the vessels were redesigned to be larger, with deeper draft, flying bridges, pump-spray systems, and greater freeboard forward to give them better seaworthiness (June, 1951). Pump-spray systems agitate the water around the vessels during fishing. To the fish, the agitated water may resemble a school of bait and partly obscure the view of the boat and fishermen.

The Hawaiian Tuna Packers, Ltd. cannery in Honolulu was established in 1917, enabling the fishery to expand beyond a relatively small fresh and dried market. The greatest annual amount sold in the fresh and dried market was 2,200 t (4.9 million lb) in fiscal year 1935 (i.e., July 1934–June 1935, Yamashita, 1958). The market for canned product allowed the fishery to expand to a peak of 6,100 t (13.4 million lb) in 1940 (Fig. 1) followed by a hiatus during WWII. From 1937 until the early 1980's most of the skipjack tuna landed in Hawaii was canned.

Before WWII the fishery included up to 26 vessels (Hudgins and Pooley, 1987) and landed an average of 5,000 t (2.3 million lb) per year from 1937 to 1940. Most vessels constructed before WWII averaged about 31 t displacement and had a bait-well capacity below 3,000 L (800 gallons, defined as Class I vessels). Larger sampans, averaging 58 t, were mostly built in the late 1940's and 1950's. These generally had a bait-well capacity greater than 3,000 L (defined as Class II vessels, Uchida, 1976; Kikkawa[1]).

As new vessels were built, fleet size increased to a maximum of 32 vessels in 1948. The prewar landings record was surpassed in 1954 (Fig. 1). During the 1950's through the early 1970's the fleet landed an average of about 4,000 t per year. Interannual variation in catch was large, but no significant long-term trend was apparent from 1948 to 1970 (Uchida, 1976).

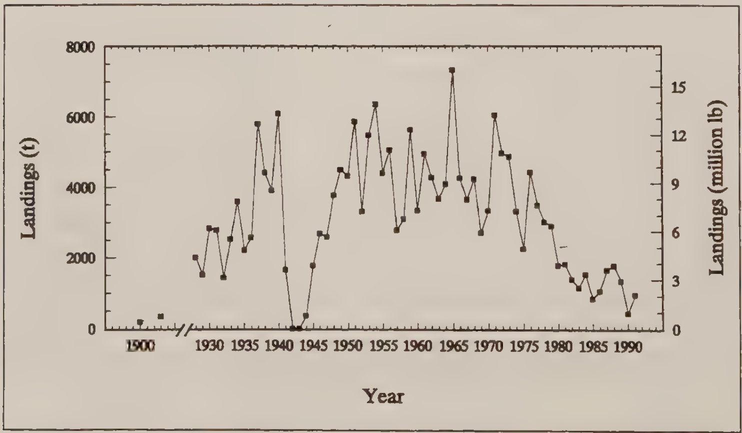

Figure 1.— Total annual skipjack tuna landings in metric tons (t) and pounds (lb) by the pole-and-line fishery in Hawaii, 1900–91. Sources: 1900–47 from Yamashita (1958); 1948–70 from Uchida (1976); 1970–83 from Kikkawa[1], 1984–85 from State of Hawaii Division of Aquatic Resources; 1986–87 from Pooley[4], and 1988–91 from Ito[3].

Total catch levels remained high despite a decline in fleet size from 32 to 15 vessels between 1948 and 1971 because 1) fishing efficiency increased as the proportion of Class II vessels in the fleet increased, and 2) the number of days fished per boat increased (Uchida, 1976). As a result, total standardized effort in the 1970's averaged only slightly below that in the 1950's (Uchida, 1976; Skillman, 1987; Kikkawa[1]) (Fig. 2).

From the 1970's to the present most of the active vessels have been the remaining wooden-hulled sampans built in the 1940's and 1950's. These vessels carry crews of 7–9 fishermen, and frequently work 6 days a week. The work is arduous and may begin with bait seining at dawn followed by fishing to dusk. One new steel-hulled vessel with about twice the displacement (91 t) of the old wooden vessels entered the fishery in the 1970's, but was not very successful.

## The Decline

Since the mid-1970's the trend in Hawaii skipjack tuna landings has been downward (Fig. 1), reflecting both a decline in fishing effort (Fig. 2) and CPUE (Fig. 3). Current (1990–91) annual landings average <1,000 t (2.2 million lb) (Ito[3]). By the mid 1980's the number of vessels in the fishery had fallen to nine (from 15 in 1971) and in 1991 only six vessels were active, four active on a full-time basis. Fishing effort dropped after 1979, falling to 1,023 Class II fishing days in 1981 and 922 days in 1986 (Fig. 2). Another major drop in fishing effort occurred in 1989–90 (Ito[3]) and 1991 effort was only 553 fishing days (Fig. 2). Fishing effort data for 1948–83

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[3] R. Y. Ito. 1992. Western Pacific pelagic fisheries in 1991. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Honolulu Lab., Southwest Fish. Sci. Cent. Admin. Rep. H-92-15, 38 p.

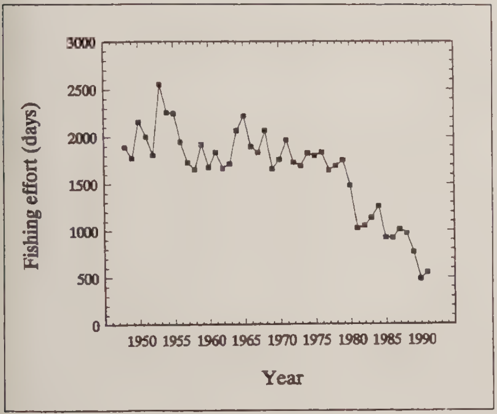

Figure 2.— Total annual fishing effort (in days) by the pole-and-line fishery in Hawaii, 1948–91. Effort data for 1948–83 and 1986–87 are standardized (Uchida, 1976; Kikkawa[1]). Sources as given in Figure 1.

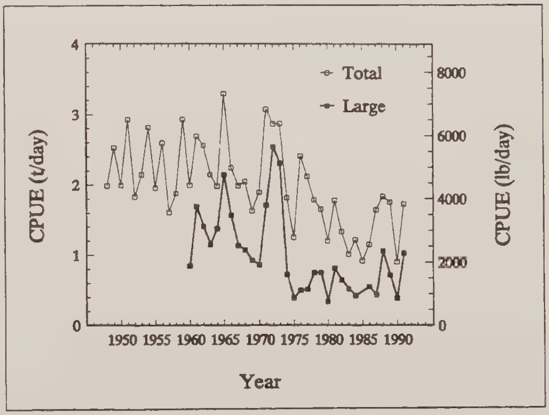

Figure 3.— Annual skipjack tuna CPUE in metric tons (t) and pounds (lb) per vessel per day for all sizes (total) and large fish (>6.8 kg or 15 lb), 1948–91. Sources as given in Figures 1 and 4.

(Uchida, 1976; Kikkawa[1]) and for 1986–87 (Pooley[4]) were standardized (Fig. 2) to account for zero-catch trips and relative efficiency (Class I versus Class II). Data for 1984–85 and 1988–91 were summary statistics without the information required for standardization. The importance of standardization was minimal after 1987 because the 1988–91 data included zero-catch trips and contained primarily Class II fishing days.

Catch rates (CPUE in t/Class II fishing day) exhibited a declining trend in the 1970's and 1980's (Fig. 3). The high degree of interannual variability in CPUE was typical of geographically restricted surface fisheries for skipjack tuna, but the declining trend was unusual. In particular, the drop in CPUE for large (>6.8 kg, >15 lb) skipjack tuna in 1974 was extreme and was sustained though 1987 (Fig. 3).

Large (>6.8 kg) skipjack tuna historically represented over 50% of the Hawaii landings by weight (Fig. 4). None of the world's major skipjack tuna fisheries depend on such large fish to supply the bulk of their catch. Large skipjack tuna command higher prices in both the fresh fish and cannery markets. From a high of over 80% in 1972–73 the proportion of large fish in Hawaii landings fell to a low of 40% in 1974 and remained below 40% through 1977 (Fig. 4). Reduced landings of large fish resulted in a substantial decrease in profitability to the pole-and-line fishery (Hudgins, 1987). The proportion of large fish in the catch has shown an upward trend since 1977 but has only exceeded 50% in a few years (1983, 1988, and 1991, Fig. 4).

The distribution of fishing effort by the fleet also changed in the 1970's. At the height of the fishery in the 1950's and 1960's, several vessels were based on the islands of Hawaii and Maui, and sizable catches came from the northeast coasts of these islands (Uchida, 1970). In the 1970's and 1980's most of the catch came from areas around Oahu, Kauai, Molokai, and Lanai (Kikkawa[1]). Presently all of the vessels work out of Kewalo Basin or Kaneohe Bay on Oahu.

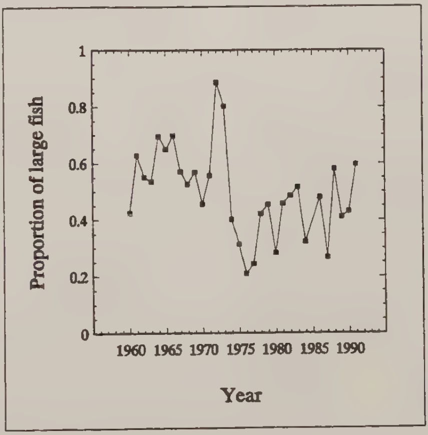

Figure 4.— The proportion of large (>6.8 kg or 15 lb) fish in annual skipjack tuna landings by the pole-and-line fishery in Hawaii, 1960–91. Sources for size composition of catches: 1960–84 and 1986–87 from Pooley[4] and 1988–91 from Ito[3].

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[4] S. G. Pooley. NMFS shore-side sampling program. Honolulu Lab., Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 2570 Dole St., Honolulu, HI 96822–2396, unpubl. data.

Increasing age of the fishing fleet and rising fuel prices may have contributed to more conservative fishing practices in the 1970's and 1980's, resulting in fewer trips taken far from land. In the 1970's skipjack tuna pole-and-line vessels also began to fish around fish aggregating devices (FAD's), in addition to the more traditional practice of scouting for bird flocks to locate fish. If large skipjack tuna were more common farther offshore, a greater frequency of nearshore trips might have contributed to the decreased catch of large fish. Uchida and Sumida (1971) found the average size of skipjack tuna caught by 7 vessels in the summer of 1967 was smallest in areas closest to Oahu.

Changes in the geographic distribution of fishing effort in the 1970's appear to have affected overall CPUE, which was consistently higher than average for oceanic areas, defined as more than 37 km (20 n.mi.) from shore (Uchida, 1966, 1970, 1976). The catch from oceanic areas averaged about 25% of the total catch from the 1950's through the early 1960's (Uchida, 1966). From 1974 to 80 catches from oceanic areas averaged only about 20% of the total catch (Kikkawa[1]). Data on the distribution of the catch in more recent years have not been summarized.

The cannery closed in 1984 because of economic restructuring in the global tuna industry and because of market constraints (King, 1987). The decline in Hawaii skipjack tuna landings contributed to the problems of the cannery but was not directly responsible for its closure. This pivotal event left the fishery with only a local, fresh and dried fish market. Previously, the fishery had been highly seasonal; summer (May–September) landings averaged about 400 t (900,000 lb) per month accounting for about 70% of annual landings (1964–82 average, Hudgins[5]). However, the fresh fish market absorbed only about 140–200 t (300,000–450,000 lb) per month after the cannery closed, reducing summer landings to about 54% of annual landings (1986–87 average, Pooley et al.[6]).

The decline of the Hawaiian domestic pole-and-line fishery roughly coincided with increases in skipjack tuna landings by the domestic troll fishery in Hawaii. The amount of skipjack tuna caught by domestic longline and handline fisheries in the Hawaii Exclusive Economic Zone (EEZ) has always been relatively insubstantial, but commercial troll catches increased from <1% of Hawaii's total skipjack tuna landings in the early 1970's to 10% in 1985 and to about 20% in 1990 and 1991. Expressed as a percentage, this increase is partly due to the decline in pole-and-line landings, but troll landings did increase from <50 t (<0.1 million pounds) in the early 1970's to >200 t (>0.5 million pounds) in 1991 (Boggs and Ito, 1993).

Pole-and-line vessels from Japan fishing for skipjack tuna within the EEZ surrounding the Northwestern Hawaiian Islands also increased their catches during the decline of Hawaii's domestic pole-and-line fishery. Foreign fishing effort increased from 213 to 767 vessel-days from 1972 to 1977, while foreign catch increased from 1,000 to 4,600 t (Yong and Wetherall, 1980). From 1978 to 1984 the annual catch in the EEZ by the foreign fishery ranged from 2,000 to 4,000 t, reaching twice the level of the domestic catch (Boggs, 1987). No foreign data have been obtained since 1984, but this fishery continued to operate legally in the EEZ through 1992. New regulations may discourage the continuation of this fishery in 1993.

## Causes for the Decline

### Bait Problems

A lack of bait during certain times of the year is frequently cited as a problem by Hawaii fishermen. The CPUE (catch per trip) for bait fish in the 1970–81 period (Kikkawa[1]) averaged slightly (ca. 4%) higher than in the previous decade (Uchida, 1977) but showed a declining trend. In 1986–88, bait fish CPUE in Pearl Harbor averaged 27% lower than that in 1970–81 (Kobayashi[7]). These modest declines (1970–81, 1981–86) in bait fish CPUE may have contributed to the problems of the pole-and-line fishery but were not viewed by industry participants as a direct cause for the decline of the fishery (Boggs and Pooley[8], 1987).

A more serious problem for some vessels has been the high cost of the vessel insurance required for entering U.S. military areas (i.e., Pearl Harbor) to catch bait (Boggs and Pooley[8], 1987). Alternatives to the harvest of wild bait by each individual vessel have been proposed (Shug and Shang[9]), but Hawaii fishermen are very resistant to purchasing bait, especially when wild bait is available. Under present conditions, the rearing or importation of bait fish would be stop-gap measures and would not be economically feasible (Shug and Shang[9]).

### Fish Availability

Owing to the small scale of Hawaii's skipjack tuna fishery, local fishing pressure is not likely to affect the availability of skipjack tuna in Hawaii. Uchida (1976) showed that in Hawaii, changes in CPUE were not associated with changes in local fishing intensity at a time when the local catch was much higher than it has been in recent years. The increase in pole-and-line catches by foreign vessels in the Hawaii EEZ in the 1970's roughly coincided with the decline of Hawaii's pole-and-line fishery (Boggs, 1987), but there was no significant correlation between annual catch by the foreign fishery in the EEZ and domestic CPUE ($r = -0.34$, $p > 0.25$, $N = 13$) for years with available data (1972–84).

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[5] L. L. Hudgins. 1986. Economic issues of the size distributions of fish caught in the Hawaiian skipjack tuna fishery 1964–82. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-86–14, 16 p.

[6] S. G. Pooley, S. Teramoto, and A. C. Todoki. 1988. Hawaii's aku boat fishery in 1986 and 1987. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-88–16, 15 p.

[7] D. R. Kobayashi. Honolulu Lab., Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 2570 Dole St., Honolulu, HI 96822–2396, unpubl. data.

[8] C. H. Boggs and S. G. Pooley. 1987. Strategic planning for Hawaii's aku industry. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-87–1, 22 p.

[9] D. M. Shug and Y. C. Shang. 1983. An economic feasibility study of culturing topminnows as an alternative baitfish for skipjack tuna fisheries in Hawaii, American Samoa, Guam, and the Northern Mariana Islands. Pacific Business Center, University of Hawaii, Honolulu, HI 96822. Econ. Dev. Admin., Tech. Assist. Proj. Rep., 32 p.

More research is needed to establish whether the Pacific-wide increase in catch from <500,000 t in 1980 to almost 900,000 t in 1990 (IATTC, 1992; Hampton, In press) has affected the availability of skipjack tuna to Hawaii fishermen. The evidence suggests major increases in catch have had no effect on relative abundance, as indicated by CPUE in large-scale fisheries. For example, the largest catch and the greatest increase in catch was in the western Pacific, where a doubling of the catch from 1980 to 1990 had no perceptible impact on CPUE in that region (Hampton, In press). Declining abundance might have been obscured by improvements in fishing efficiency that increase CPUE (Hampton, In press). However, tagging experiments in the western Pacific also suggest that skipjack tuna are too productive to be affected by current levels of harvest (i.e., <1 million t). Kleiber et al. (1983) estimated a western Pacific biomass of skipjack tuna on the order of 3 million t and a turnover rate of 6 million t/year. These studies (Kleiber et al., 1983; Hampton, In press) imply that the decline in Hawaii CPUE was not caused by a decline in the abundance of skipjack tuna in the western Pacific.

Some genetic evidence suggests that skipjack tuna in Hawaii are part of a central and eastern Pacific stock that is partially isolated from the western Pacific resource (Matsumoto et al., 1984; Kearney, 1987). Tagging experiments in the eastern Pacific have resulted in tag recoveries in Hawaii, whereas western Pacific tagging experiments have not (Kearney, 1987). Therefore, the decline in Hawaii's CPUE (Fig 4) might logically be attributed to a corresponding increase in eastern Pacific skipjack tuna catches (Hudgins[5], 1987) which exceeded previous (1960–74) levels in 1975 and remained higher than average through 1982 (IATTC, 1992). However, the timing of this increase could not correctly explain the decline in catches in Hawaii a year before (in 1974). Moreover, eastern Pacific catches subsequently declined (1983–90, IATTC, 1992) without a corresponding increase in Hawaii's CPUE (Kearney, 1987). Furthermore, CPUE in the eastern Pacific seems to be unaffected by harvest level (IATTC, 1992).

If there was a negative impact of the eastern Pacific fishery on Hawaii's fishery, it would most likely take effect after a time lag to give eastern Pacific fish time to reach Hawaii and to grow to the size harvested by Hawaii's fishery (Kearney, 1987). A significant ($r = 0.54$, $p < 0.05$, $N = 30$ years) negative correlation has been found between the Hawaii catch of skipjack tuna and the total catch (of all sizes) in the eastern Pacific one year earlier (Ianelli[10]). However, a better indicator of interaction between these fisheries would be a significant negative correlation between CPUE (rather than catch) in Hawaii and the eastern Pacific catch in the preceding year. No such correlation has been found (Kearney, 1987; Ianelli[10]).

The unusual dependence of Hawaii's skipjack tuna fishery on large fish means that it is more sensitive to changes in fish population size structure than the large-scale fisheries of the eastern and western Pacific. A reduced size-frequency distribution of the population due to increasing harvests by large-scale fisheries might not be reflected in the CPUE of those fisheries but still affect availability of large skipjack tuna in Hawaii (Boggs, 1987). Eastern Pacific skipjack tuna size-frequency distributions show decreasing average size from 1972 to 1981 followed by increasing average size through 1985 (IATTC, 1985, 1992). This sequence does not correspond closely with Hawaii's abruptly reduced proportion of large fish in 1974, or the increasing trend after 1977 (Fig. 4). Further analyses of these data are being conducted (Ianelli[10]). In the western Pacific, improved collection and analysis of size-frequency data are needed for evaluation of fishery interaction (Hampton, In press).

Annual time series of skipjack tuna catch in Hawaii have been found to be correlated with sea surface temperature (Jones[11]) and salinity (Seckel, 1972). Various models have been used to predict annual catches based on these environmental variables (Mendelssohn[2]; Boggs, 1988, 1989). The most recent model based on sea surface temperature (Boggs, 1988) explained 68% of the variation in the CPUE of large skipjack tuna during 1960–83 (Fig. 5). This model suggests that a sustained decline in CPUE for large skipjack tuna after 1973 was related to a sustained change in spring sea surface warming patterns east of Hawaii.

Spring warming patterns reflect the relative strength and northward extent of the California current extension (CCE) which joins the North Equatorial Current (NEC) near Hawaii. An hypothesis is that the CCE and NEC provide a conduit for immigration of large skipjack tuna from the eastern tropical Pacific to Hawaii (Seckel, 1972; Boggs, 1988). The most recent models also involve a time lag (Mendelssohn[2]; Boggs, 1988) which could reflect relationships between temperature and recruitment, mortality, or migration in preceding years. Previous models (e.g., Seckel, 1972) explained variation in Hawaii CPUE based on the proximity of the north edge of the CCE or NEC as measured by sea surface temperature and salinity in Hawaii, but these models eventually failed to provide good predictions when the north edge of the current passed north of the islands (Skillman[12]).

The spring warming model (Mendelssohn[2]; Boggs, 1988) was used to predict CPUE for large skipjack tuna during 1984–90 and indicated that the availability of large skipjack tuna

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[10] J. Ianelli, Fisheries Research Institute, Univ. Wash., Seattle, WA 98195. 1992, personal commun.

[11] E. C. Jones. A winter index of Hawaiian skipjack tuna catch. Honolulu Lab., Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 2570 Dole St., Honolulu, HI 96822–2396, unpubl. manuscr.

[12] R. A. Skillman, Honolulu Lab., Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 2570 Dole St., Honolulu, HI 96822–2396. 1991, personal commun.

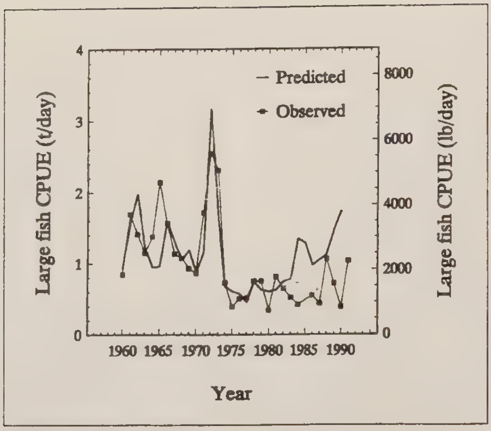

Figure 5.— Annual skipjack tuna CPUE in metric tons (t) and pounds (lb) per vessel per day for large fish (>6.8 kg or 15 lb), 1960–91, compared with CPUE predicted by an environmental model. Sources as given in Figures 1 and 4.

around Hawaii should have returned to pre-1974 levels after 1983 (Fig. 5). Although the proportion of large fish in the Hawaii catch returned to 1960–73 average levels in 1988 and 1991 (Fig. 4), the CPUE for large skipjack tuna in recent years has remained much lower than predicted (Fig. 5).

Three factors that may have contributed to lower-than-predicted CPUE after 1983 were 1) a self-imposed quota employed by vessels to avoid flooding a limited market, 2) reduced scouting and fishing closer to port, and 3) a change in the overall age structure of the population because of increased fishing pressure elsewhere in the Pacific. The first two factors are economic, and could result in reduced CPUE without any change in fish abundance. For example, CPUE is biased downwards by a self-imposed quota (factor 1) because measures of effort (days) and CPUE (catch per day) do not account for trips of less than a day when a quota is achieved early in the day. Increased fishing near shore (factor 2) would decrease CPUE because average CPUE is highest >37 km from shore (Uchida, 1966, 1970, 1976) and fish may be smaller than average near shore (Uchida and Sumida, 1971). Existing analyses do not indicate that the availability of large fish has been reduced by the impacts of fishing on population age structure (factor 3) but further study is needed.

## Economic Causes of the Decline

One economic factor in the continuing decline in total catches after 1974 (Fig. 1) was a negative correlation between catch and the price of fuel (Hudgins[5]). In a comparison of catches for 1982 with those for 1974, the decrease in annual catch attributable to fuel price increases was estimated to have reduced annual revenue by $1.3 million. Over this same period, a decrease in catch attributable to reduced CPUE and a low proportion of large fish in the catch (Fig. 4) were estimated to have reduced annual revenue by $1.0 and $0.36 million, respectively (Hudgins[5]). These losses represent over 50% of potential revenue; actual revenue was only $2.5 million in 1982 (Pooley et al.[6]).

The mechanism by which fuel price increases affect the catch has not been documented, but the fuel price rise that began in 1973 did not immediately affect the total number of fishing days (Fig. 2). Perhaps expensive fuel and poor maintenance on some vessels result in restricted scouting for schools of fish and in fishing closer to land. Fishing around FAD's may increase the proportion of small fish in the catch (Boggs and Pooley, 1987), but FAD fishing seems to be mostly a last resort when schools of larger fish cannot be located. Small fish landings increased in 1976 whereas FAD's were not fully deployed until 1980 (Hudgins[5], 1987).

Declining profitability has played an important role in the decline of the fishery (Pooley, 1987). Low earnings since the 1960's curtailed investment in new boats. Attempts to increase profits by selling more high-priced, fresh skipjack tuna faced market limitations even before the cannery closed. During 1970–85 the price per ton rose 45%, but costs rose 75% (after inflation). To offset fuel (200%) and insurance (390%) cost increases, the share of profit paid to crews was kept low, and repairs were postponed (Pooley, 1987). Poor maintenance resulted in frequent breakdowns and safety problems. Five vessels which sank during the 1980's and 1990's have not been replaced. Such problems may have influenced the fleet's fishing range, resulting in fewer fishing trips to more productive oceanic areas. Now, most of the vessels still remaining in the fleet are well maintained.

An increase in troll, handline, and longline landings of yellowfin and bigeye tunas during the 1970's and 1980's resulted in competition for the fresh tuna market, reducing the available market for skipjack tuna after the cannery closed. Although skipjack tuna is priced lower than yellowfin tuna (on average) and is appreciated by Hawaii residents in raw, cooked, and dried product forms, it is not widely accepted in the local restaurant (tourist) or export markets. In 1985 the average ex-vessel price for skipjack tuna was only $2.48/kg ($1.13/lb), whereas the average price for yellowfin tuna was 26% higher. The price difference has increased along with prices, and in 1991 the average yellowfin tuna price of $4.98/kg ($2.26/lb) was 58% higher than the average skipjack tuna price. Yellowfin tuna can readily be sold to the restaurant market in Hawaii or exported, and it has a much longer shelf life than skipjack tuna. Yellowfin and bigeye tuna are preferred over skipjack tuna for sashimi in the export markets. Flash-frozen skipjack and yellowfin tuna imported to Hawaii from Japan also competes with the Hawaii fishery for a share of the local market. The flash-frozen product is acceptable for sashimi, although it can be distinguished from fresh skipjack tuna.

The closure of the Honolulu tuna cannery in 1984 cost the skipjack tuna fishery an estimated $0.5 million (18%) in annual sales, and the loss would have been much worse had the fishery not already been so reduced (Hudgins, 1987). The most pronounced effect of the closure has been to discourage revitalization of the fishery. The lack of a cannery market is especially troublesome during the summer when the skipjack and yellowfin tuna fisheries reach peak production. As a result, pole-and-line vessels occasionally experienced severe market competition and devastating price reductions in the 1980's (Boggs and Pooley, 1987).

Self-imposed catch limits are now employed by Hawaii pole-and-line vessels to avoid flooding the limited fresh-fish market, especially on trips made during summer when fish are most available (Boggs, 1988, 1989). Incorporation of a monthly limit to landings with an environmental model (Boggs, 1988) produced more realistic predictions of CPUE and annual catch (Boggs, 1988, 1989). Since summer is also the season when large fish predominate in the catch, self-imposed quotas contribute to a lower proportion of large fish on an annual basis.

In summary, Hawaii's pole-and-line fishery was economically stressed throughout the 1970's and 1980's because of rising costs and reduced profitability (Pooley, 1987). Then from 1974–83 the availability of large fish declined because of environmental changes (Mendelssohn[2]; Boggs, 1988) and the fishery declined. Models based on environmental factors predict increased availability since 1983 but CPUE has remained low. Reasons for continuing low CPUE may include self-imposed quotas and fishing closer to shore than in the past. No clear evidence indicates that overfishing has had a negative impact in Hawaii or elsewhere in the Pacific. The fishery has not recovered owing to continued high costs, low profits, and a limited market.

### Remedies and Future Prospects

A workshop and a strategic planning process (Boggs and Pooley[8], 1987) were conducted in Honolulu in 1986 to discuss causes of the fisheries decline and remedial actions. An expanded market and products with a long shelf life to absorb peak production during the summer were seen as the most important objectives for revitalizing the fishery. A group of investors purchased the cannery facility in 1985 with the intention of integrating it into a marine-oriented tourist center but the cannery has not reopened. Making tuna canning profitable in Hawaii would require promotion of specialty packs that appeal to tourists and local residents, because production of normal canned tuna in Hawaii is too expensive to compete on the world market (King, 1987).

The available evidence indicates that the skipjack tuna population can easily support an expanded fishery in Hawaii, although the fishery would remain vulnerable to an environmentally driven reduction in availability like that of 1974–83. If ocean-wide fishing pressure has had an impact on availability, local (EEZ) management would not substantially ameliorate that impact because the local fishery is relatively small. Bait fish stocks would be the only resources that might require local management if the fishery were to expand. These stocks were sufficient in the 1970's to support three times the number of full-time vessels currently active. The modest decline of bait fish stocks (ca. 27%) since the 1970's might become a limiting factor if the fishery were to more than double its present size. If the profitability of the fishery increased, it might be able to support a bait fish culture industry (Shug and Shang[9]).

The future of the fishery depends primarily on the development of markets. The State of Hawaii has conducted market expansion projects and supported experiments to try and increase product shelf life, but these have not been very successful, in comparison with similar efforts in promoting other species. Expansion of the market will likely require innovative product technology that can economically preserve summer catches for later sale or fishing technology that will permit increased catches during the season of low availability.

In 1986 Hudgins (1987) predicted that without new markets, economic competition would force all but 4 or 5 of the most efficient Hawaii skipjack tuna fishing vessels out of business. She predicted that these vessels would supply about 900 t (2 million lb) of the skipjack tuna in the Hawaii fresh market at prices of $2.75–3.85 per kg ($1.25–1.75/lb). These predictions are almost exactly met by the number of vessels (6, 4 full-time), landings (955 t, 2.1 million lb), and average price ($2.87/kg, $1.30/lb) for skipjack tuna in 1991. Unless a larger market is developed, there is no reason to expect much expansion of Hawaii's skipjack tuna fishery in the near future. The pole-and-line fleet may continue to decline with age and the local market may increasingly be supplied by imports and by Hawaii's commercial troll fishery.

### Acknowledgments

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# Effects of entanglement and escape from high-seas driftnets on rates of natural mortality of North Pacific albacore, *Thunnus alalunga*

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North Pacific albacore (*Thunnus alalunga*) are heavily fished and may have experienced recent reductions in recruitment (NOAA, 1991). U.S. troll fishery landings and catch per unit of effort (CPUE) have been decreasing since the 1960's and are currently at only about 50% of their peak levels (Kleiber and Perrin, 1991; NOAA, 1991). Landings and CPUE by the Japanese pole-and-line fishery have also been falling continuously since the late 1970's[1]. North Pacific albacore are additionally targeted by longline fleets, and considerable numbers are taken by high-seas large- and small-mesh driftnet fleets. The small-mesh fleets of Japan, Taiwan, and Korea target neon flying squid (*Ommastrephes bartramii*) and incidentally capture albacore. The large-mesh fleets of Japan and Taiwan target albacore, skipjack tuna (*Katsuwonus pelamis*), and various billfishes (*Istiophoridae* and *Xiphiidae*).

Foreign driftnet fleets and U.S. trollers taking albacore overlap geographically (Fig. 1). They also target a common stock even when fishing in widely separated areas because of the trans-Pacific migration of albacore (Otsu and Uchida, 1963). Albacore that encounter drift nets, and escape to survive long enough to be recaptured by another fishery can bear some external marks[2,3]. These marks provide direct evidence of interactions among fisheries. U.S. trollers operating in the North Pacific have reported an increased frequency of net-marked fish with the expansion of the Taiwanese, Korean, and Japanese high-seas driftnet fleets (NOAA, 1991;[2,3]).

Albacore that become entangled in drift nets face a number of possible fates (Fig. 2). The fraction that become entangled and subsequently drop out (alive or dead) is not known. If it is significant, the North Pacific albacore stock could be affected more seriously by high-seas drift nets than landings alone indicate. Our study, part of a larger effort to determine the impacts of drift nets on the North Pacific albacore stock, was undertaken to determine whether albacore that encounter drift nets, and subsequently escape alive, suffer higher than normal rates of natural mortality.

Our strategy was to look for differences in measures of fitness, and differences in short-term and long-term growth rates between net-marked (i.e., fish that have encountered drift nets and escaped) and unmarked albacore. We also looked for indications of bacterial infection and long-term stress in net-marked albacore. These parameters could evince, although not quantify, differences in rates of natural mortality. We had to use indirect measures because rates of natural mortality (or physiological changes) could not be directly observed in albacore encountering simulated drift nets in shoreside tanks. Unlike skipjack and yellowfin tuna (*Thunnus albacares*) (Brill, 1992), albacore have yet to be successfully maintained in captivity.

Selection of specific parameters was constrained by the necessity of collecting measurements and samples at sea aboard small commercial fishing vessels. We could acquire only measurements and samples that could be obtained under difficult conditions and that did not interfere with normal fishing operations. We were further limited to collecting samples that could be stored for later processing in the laboratory and that would not reduce the market value of the catch. Given these constraints, we chose the following parameters. Weight to length and maximum girth to length ratios were used as indicators of general fitness (Bolger and

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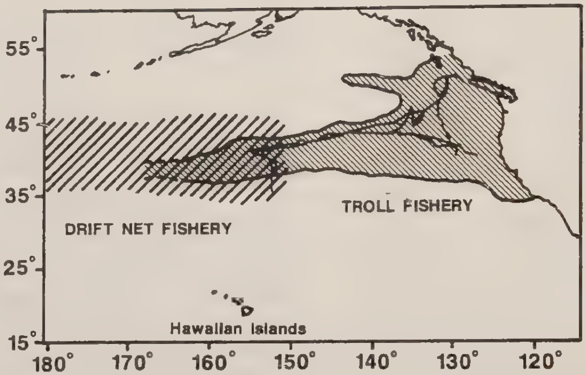

Figure 1

Area of operation of the U.S. troll fishery (light cross-hatching) catching albacore. Track lines of U.S. vessels carrying National Marine Fisheries Service observers in 1991 are shown by the solid line. Area of operation of foreign drift net fleets (heavy cross-hatching) extends west to approximately 140°W.

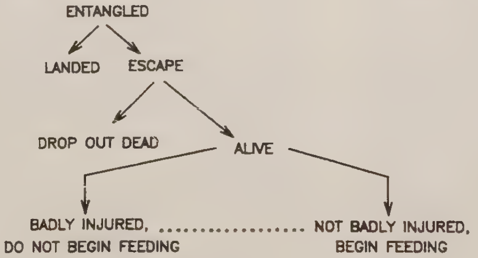

Figure 2

The possible fates of albacore that become entangled in high-seas drift nets. Note that the condition of fish which escape drift nets alive probably form a continuum from those that are so badly injured that they succumb quickly, to those that are only slightly injured and resume feeding immediately.

Connolly, 1989; Cone, 1989, 1990; Murphy et al., 1991). Relative otolith weight (i.e., the ratio of otolith weight to body weight) was used as an indicator of long-term growth rate (Boehlert, 1985; Pawson, 1990; Fletcher, 1991). (Because otolith weight is proportional to fish age rather than to body size, slower-growing fish have larger otoliths at a given body size because they have taken longer to reach that body size.) RNA:DNA ratio of white muscle was measured because it is an established indicator of short-term (days to weeks) growth rates (Bulow, 1970; Bulow et al., 1981; Ferguson and Danzmann, 1990; Mustafa et al., 1991). Relative leukocyte abundance (i.e., the ratio of leukocytes to red blood cells) was assessed as an indicator of bacterial infection and long term stress (Blaxhall, 1972; Anderson, 1990; Goede and Barton, 1990). Although muscle lipid content can be used as a measure of recent feeding history (Dotson, 1978), it was not used in this study. The lipid content of tuna muscle is dependent on sampling site (Dotson, 1978; Vileg et al., 1983; Boggs and Kitchell, 1991) and this factor could not be rigorously controlled.

## Materials and methods

During 1990 and 1991, observers were placed aboard ten U.S. trollers by the Southwest Fisheries Science Center (NMFS, NOAA), in cooperation with the Western Fishboat Owners Association. Observers documented the number of net-marked albacore landed and collected data and samples for our study. Boats operated in an area of the North Pacific shown in Figure 1. Albacore were classified according to the severity of net damage with a scheme (Table 1) developed by Bartoo et al.[2]. Fork length, maximum girth (both to the nearest centimeter), and body weight (to the nearest kilogram) were measured. Dried blood smears, sagittae (otoliths), and white-muscle samples (frozen in sealed tubes in the boats' commercial fish freezers) were also obtained from a subsample of landed fish selected by the observers. Muscle samples (taken from the small amount of muscle remaining near the skull following decapitation) and otoliths could be obtained only on vessels that processed (i.e., "gilled and gutted") their catches. Complete sets of samples were not, therefore, obtained from every fish.

In the laboratory, otoliths were dried, cleaned, and weighed to the nearest 0.1 mg on a Sartorius 1207 MP2 electronic balance. RNA and DNA were extracted from the frozen muscle samples by standard procedures (Hutchison and Munro, 1961; Munro and Fleck, 1966; Wilder and Stanley, 1983). The only modifications were that the RNA was extracted with 1.0 N NaOH, and the DNA with 1.2 N perchloric acid, both at 37°C for 60 minutes. RNA, DNA, and protein concentrations were measured with a Beckman model 35 UV spectrophotometer using the dual wave length method (Tsanev and Markov, 1960) and standard extinction coefficients (Wilder and Stanley, 1983). Red cells and leukocytes were counted in Geimsa-stained blood smears with the aid of light microscopy (oil immersion lens) in a minimum of three microscope fields, or until at least 200 red cells were counted. Eosinophils could be easily differentiated from the remainder

**Table 1**

Net damage classification scheme (Bartoo et al.[2]) used to assess severity of injury to albacore caused by entanglement and escape from drift nets, and the number fish in each damage code category examined for our study.

| Damage code | Damage description | Number of fish |
|---|---|---|
| 0 | No damage or scarring. | 217 |
| 1 | Minor damage along side(s) of fish, pattern of stripes due to minor scale loss where fish forced its way through or along the net. | 39 |
| 2 | Minor damage to head, chiefly forward of pectoral fins, brush-like pattern of scale loss. | 5 |
| 3 | Severe damage from bruising or scraping away of parts of the skin, primarily in area of greatest girth and mostly on dorsal surface. | 10 |
| 4 | Damage of any degree that was partially or completely healed. | 60 |

of the leukocyte population and were excluded from the total leukocyte count. Although Alexander et al. (1980) described the distinguishing features of albacore blood cells, we were only able to differentiate eosinophils clearly from the remainder of the leukocytes. Leukocytes were, therefore, not further classified.

By using data from unmarked fish only, regressions of body weight on fork length, maximum girth on fork length, and otolith weight on body weight were fitted by a least squares procedure (Statgraf Statistical Software) to the exponential equation:

$$Y = a \cdot x^b.$$

Regression parameters a and b were estimated for each case.

Relative condition factor, relative girth, and relative otolith weight for individual fish were then calculated with the regression parameters:

$$K = W/(a \cdot X^b).$$

When $K$ = relative condition factor, $W$ = body weight and $X$ = fork length; when $K$ = relative girth, $W$ = maximum girth and $X$ = fork length; and when $K$ = relative otolith weight, $W$ = otolith weight and $X$ = body weight.

Relative condition factor, relative girth, and relative otolith weight were calculated to permit direct comparison of groups containing individuals of different body sizes (Pollard, 1972; Brill et al., 1987).

The standard condition factor ($C$) was calculated separately for unmarked and net-marked fish:

$$C = W / FL^3$$

where $W$ = body weight and $FL$ = fork length.

Fish were grouped only as net-marked (damage codes 1-4, Table 1) and unmarked (damage code 0). Differences in mean values for unmarked and net-marked fish were evaluated by unpaired Student's $t$-tests with $P < 0.05$ taken as the maximum level for statistical significance.

## Results and discussion

The only significant differences between net-marked and unmarked fish were in measures of absolute size (mean fork length, body weight, and maximum girth), which were greater for unmarked albacore (Table 2). These data suggest that smaller fish escape drift nets, survive, and are recaptured by the troll fleet more frequently than large fish. This appears to be confirmed by size-frequency distributions for the 217 net-marked and 114 unmarked fish included in this study (Fig. 3A). The two peaks in Figure 3A (at approximately 65 and 80 cm) represent 3- and 4-year-old fish, respectively[2] and imply that 4-year-old individuals predominate the unmarked group. In the net-marked group, 3- and 4-year-old fish are approximately equally represented. This result is, however, more likely due to either a sampling bias of the observers when choosing fish for inclusion in this study, or to time-area variations in fish size composition and the percentage of net-marked fish. The size-frequency distributions of

**Table 2**

Parameters measured to evaluate the effects of escapement from drift nets on the natural mortality of albacore *Thunnus alalunga*. *N* equals the number of observations.

| | Unmarked fish | | Net-marked fish | |
|---|---|---|---|---|
| Parameters | Mean ± SD | *N* | Mean ± SD | *N* |
| Body weight* (kg) | 10.6 ± 2.4 | 182 | 8.6 ± 2.6 | 83 |
| Fork length* (cm) | 79.1 ± 7.4 | 215 | 73.5 ± 7.9 | 114 |
| Maximum girth* (cm) | 56.1 ± 5.7 | 214 | 51.8 ± 6.2 | 113 |
| Condition factor (kg/cm$^3$) | 0.0208 ± 0.0015 | 182 | 0.0210 ± 0.0017 | 83 |
| Relative girth | 1.00 ± 0.02 | 214 | 1.00 ± 0.03 | 113 |
| Relative condition factor | 1.00 ± 0.07 | 182 | 1.00 ± 0.07 | 83 |
| RNA to DNA ratio | 6.99 ± 0.97 | 34 | 6.90 ± 1.49 | 36 |
| Relative otolith weight | 1.00 ± 0.09 | 175 | 0.99 ± 0.11 | 47 |
| Leukocytes/200 red cells | 7.26 ± 5.30 | 15 | 6.44 ± 3.59 | 35 |

*$P \le 0.05$.

a much larger number of albacore (12,085 unmarked and 381 net-marked individuals[4]; and from which the fish used in this study are a subsample, show that the frequency distributions of 3- and 4-year-old net-marked and unmarked fish are more nearly identical (Fig. 3B); 3-year-old fish were found to be only slightly dominant in both groups.

Our objective in calculating condition factor, relative girth, and relative condition factor (also referred to as relative weight) was to determine if there was any indication of differences in fitness between unmarked and net-marked fish. No differences were found (Table 2). The use and misuse of condition factor and relative condition factor have received much recent attention (Bolger and Connolly, 1989; Cone, 1989; Murphy et al., 1991). The use of such indices in groups of fishes with different mean lengths and size-frequency distributions may not be justified because disparities may be due to differences in body size, rather than to physiological fitness (Cone, 1989, 1990). Because indices of fitness were not different for unmarked and net-marked fish, we considered the question of suitability moot.

No differences were found either in measures of short-term (RNA:DNA ratio) or long-term (relative otolith weight) growth rates (Table 2). The RNA:DNA ratio can be affected by the age of the fish (Haines, 1973); however, it was not corrected for body size (i.e., age) because we found no correlation between it and body weight.

The relative leukocyte counts also did not differ between unmarked and net-marked albacore (Table 2). We assumed that net-marked albacore could show either elevated or reduced leukocyte counts. Acute bacterial infection has been shown to increase leukocyte counts in fish (Wedemeyer et al., 1990). Conversely, reduced leukocyte counts can be caused by elevated circulating corticosteroid levels (an acute stress response) or by chronic bacterial infection causing leukocytolysis (Shreck, 1981; Wedemeyer et al., 1983). The lack of difference between unmarked and net-marked albacore suggests that none of the processes that can affect relative leukocyte counts was occurring in the latter.

We were hampered in interpreting our results because we could not determine precisely how long the fish were at liberty following escapement from drift nets. Based on observations of skipjack and yellowfin tuna held in shoreside tanks at the Kewalo Research Facility (described in Brill, 1992), skin damage resulting from capture generally heals completely within weeks in feeding fish (R. W. Brill, unpubl. observations). Fish with damage codes 1–3 (Table 1), therefore, probably encountered drift nets within one month of recapture. It was impossible to estimate how long fish with damage code 4 had been at liberty or how long net damage remains visible, although Bartoo et al.[2] speculated that fish with damage code 4 may have been at liberty more than a year since encountering a

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[4] N. Bartoo, D. Holts, C. Brown, and L. Halko. La Jolla Laboratory, Southwest Fish. Sci. Cent., unpubl. data.

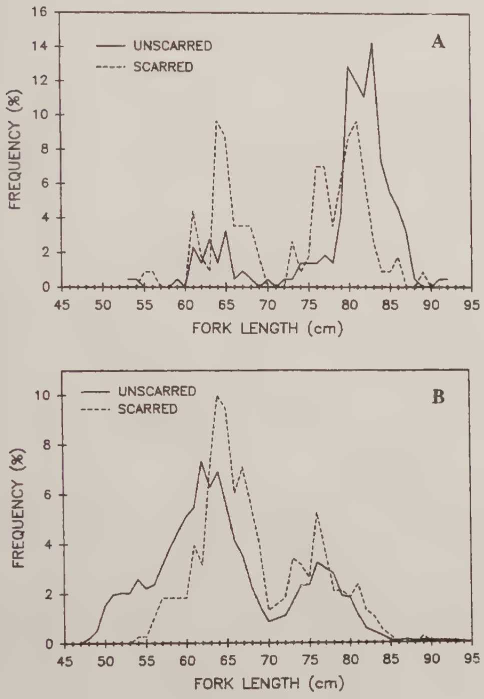

**Figure 3**

Size-frequency distribution of the unmarked and net-marked albacore sampled for our study (**A**) (215 unmarked and 114 net-marked fish) and much larger data set (**B**) (12085 unmarked and 318 net-marked fish) from which the fish used in our study are a subset (N. Bartoo, D. Holts, C. Brown, and L. Halko, SWFSC, La Jolla Laboratory, unpubl. data).

drift net. It is unknown if this is sufficient time for differences in relative otolith weight to become measurable. Boggs and Kitchell (1991) showed that significant weight loss occurs in tunas within one week of starvation. Therefore, it was likely that net-marked fish were at liberty long enough for measures of physiological fitness to become apparent, assuming net-marked albacore had not been feeding prior to recapture. The rate at which relative leukocyte abundance changes in albacore following stress or infection is not known, but in coho salmon (*Oncorhynchus kisutch*) and rainbow trout (*O. mykiss*) leukocyte abundance changes within 96 hours of imposition of stressful conditions (McLeay and Gordon, 1977). Leukocyte abundance should be a good measure of differences in the health of net-marked and unmarked albacore, but the large standard deviation (Table 2) may limit its usefulness in this species.

Failure to detect differences (Table 2) between unmarked and net-marked albacore suggests that the fish escaping from drift nets, and living long enough to become vulnerable to recapture by U.S. trollers, do not suffer increased natural mortality. Most of the fish however, recaptured by trollers are found to be only minimally damaged or to have healed scars (Table 1), which may explain the lack of differences between net-marked and unmarked fish. As shown in Figure 2, there is most likely a spectrum of damage caused during encounters with drift nets. We do not know if the distribution of damage severity in the population of albacore vulnerable to the troll fishery is the same as that of all the albacore that escape drift nets alive. Also, the number of albacore falling out dead, or escaping so badly injured that they succumb before becoming vulnerable to recapture by troll vessels, may well be significant but remains to be determined.

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# Vertical and horizontal movements of striped marlin (*Tetrapturus audax*) near the Hawaiian Islands, determined by ultrasonic telemetry, with simultaneous measurement of oceanic currents

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**Abstract.** We measured the vertical and horizontal movements of striped marlin (*Tetrapturus audax*) off the leeward coast of the Island of Hawaii between 20 November and 18 December 1992 while simultaneously gathering data on water temperature and oceanic currents. Fish movements were monitored by ultrasonic depth-sensitive transmitters, depth-temperature profiles by an expendable bathythermograph system, and oceanic current patterns by an acoustic Doppler current profiler. Like Indo-Pacific blue marlin (*Makaira mazara*), striped marlin near Hawaii spend >85% of their time in the mixed layer (i.e., above 90 m depth). The maximum depth for striped marlin appears to be limited by water temperatures 8 C° colder than the mixed layer, rather than by an absolute lower temperature. We also found that the horizontal displacements of some striped marlin can be strongly influenced by currents.

## Introduction

Striped marlin (*Tetrapturus audax*) are widely distributed in the Pacific and Indian Oceans, but are absent from the Atlantic Ocean (Ueyanagi and Wares 1974, Squire and Suzuki 1990). Like other members of the Istiophoridae, striped marlin are large pelagic predators which make extensive movements. They are not, however, considered as highly migratory as bluefin tuna (*Thunnus thynnus*) or albacore (*T. alalunga*), which undertake rapid and regular transoceanic migrations (Squire and Suzuki 1990). Also, like other members of the Istiophoridae, striped marlin are apparently adapted for attaining and rapidly recovering from extraordinary peak levels of activity, rather than for sustaining high cruising speeds (Johnston and Salmonski 1984, Daxboeck and Davie 1986, Wells and Davie 1986, Wells et al. 1986, Davie 1990). Recently, direct measurements of swimming speeds of Indo-Pacific blue marlin (*Makaira mazara*[1]) confirmed that this species spends the majority of its time moving at relatively slow, and presumably aerobically sustainable, speeds (Block et al. 1992a).

Data are available on the short-term vertical and horizontal movements of striped marlin near the California coast. Holts and Bedford (1990) tracked 11 striped marlin and found that these fish spend most of their time in the mixed layer (19 to 20 °C) and only occasionally descend into water where the temperature is <12 °C. Five of the eight marlin followed for 20 to 48 h moved predominately in one direction at an average ground speed of 1.18 knots (0.607 m s$^{-1}$). The other three fish remained in the vicinity where they had been initially captured and released.

Prior to our study, no information was available on the short-term vertical and horizontal movements of striped marlin near the Hawaiian Islands, an environment quite different from the waters off California (McGary 1955, Seckel 1955, Lynn et al. 1982, Holland et al. 1990a, b, Holts and Bedford 1990). Comparison of the vertical movements and depth distributions of striped marlin near California and Hawaii can reveal factors limiting vertical distribution of this species. Data on vertical movements is additionally useful for resource conservation and fisheries' management. For example, knowledge of the depth distributions of billfishes can enable commercial longline fleets to alter their gear (i.e., adjust hook depths) to minimize the catch of particular species.

Our study also provides the first description of the movements of pelagic fish with simultaneously gathered data on the speed and direction of oceanic currents obtained directly using an acoustic Doppler current profiling system. Previous studies using ultrasonic telemetry to determine tuna and billfish activities (e.g. Yuen 1970, Laurs et al. 1977, Carey and Robinson 1981, Holland et al. 1990 a, b, Holts and Bedford 1990) reported rates of movement which were actually speed over ground (i.e., speed was calculated from positional data) rather than true swimming speed (i.e., speed through the water). Also, without data on oceanic currents, no conclusions could be drawn as to the effects of currents on horizontal displacements. Block et al. (1992 a) partially circumvented these problems by employing telemetry transmitters capable of directly measuring the swimming speed of Indo-Pacific blue marlin, but they lacked a quantitative measurement of currents. Carey and Scharold (1990) directly telemetered swimming speeds of blue sharks (*Prionace glauca*) with current speed and direction estimated from the drift of fishing gear and satellite sea-surface temperature images. These investigators found that both the speed and direction of blue shark movements can be strongly influenced by currents.

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[1] The common and scientific names for the billfishes used herein follow Nakamura (1985), whereby Atlantic and Indo-Pacific blue marlin are recognized as separate species: *Makaira nigricans* and *M. mazara*, respectively.

## Materials and methods

Two research vessels were employed during our study, the 11 m "Kaahele'ale" and the 53 m National Oceanic and Atmospheric Administration (NOAA) ship "Townsend Cromwell". The hydrophone mounting system aboard the "Kaahele'ale" has been described previously (Brill et al. 1984, Holland et al. 1985). The system aboard the "Townsend Cromwell" was a four-hydrophone array (VEMCO, Halifax, Nova Scotia, Canada) mounted beneath a modified fiberglass depressor wing (V-FIN, Environmental Devices Corporation, Marion, Massachusetts, USA). During tracking operations, the depressor wing was towed amidships ≅5 m beneath the surface. Hydrophones were selected individually by a four-position switch mounted near the receiver.

*Tetraptures audax* were captured by standard commercial monofilament longline gear between 20 November and 18 December 1992. Fishing operations were conducted off the western coast of the Island of Hawaii (156°00'–157°00'W; 19°15'–20°15'N) because the high volcanoes provide a lee of up to ≅10 nautical miles (18.5 km), from the strong northeasterly trade winds. About 120 baited hooks, attached to ≅ 3 to 6 nautical miles (6 to 11 km) of longline, were deployed from the "Townsend Cromwell", soaked for 4 to 8 h, and then retrieved. Individual fish were identified to species and body weights estimated independently by two experienced observers (R. W. Brill and D. B. Holts). Striped marlin that appeared healthy were brought alongside the ship and an ultrasonic depth-sensitive transmitter (VEMCO, Halifax, Nova Scotia, Canada, Model VP-3) was attached to the anterior dorsal musculature using a standard tagging pole. The transmitter attachment system employed the stainless arrowhead design used previously by Holland et al. (1990 a). Immediately after attachment of the transmitter, the fish was released by cutting the leader as close as practical to the fish. No attempt was made to retrieve the hook. Individuals were initially followed by the "Kaahele'ale" until the remainder of the longline gear had been retrieved (usually 1 to 2 h). The "Townsend Cromwell" would then join the other vessel and the fish were tracked in tandem.

The transmitters encoded depth information by varying pulse interval. The output from the transmitters was received aboard both vessels by VEMCO VR-60 ultrasonic receivers. The audio output from the receiver aboard the "Kaahele'ale" was recorded by a standard audio-tape deck. Aboard the "Townsend Cromwell", a frequency counter and IBM PC were used to measure and convert every other pulse interval to depth, and to store the data digitally. The audiotapes recorded aboard the "Kaahele'ale" were later digitized by the computer system aboard the "Townsend Cromwell".

Positional information was obtained aboard both vessels using global positioning system (GPS) satellite receivers. Aboard the "Townsend Cromwell", positional information was also obtained using a satellite navigation system (SATNAV) receiver, LORAN-C receiver, and radar fixes from the nearest point of land. The ships' positions were assumed to be the same as that of the fish and were recorded approximately every 15 min. Oceanic current data (absolute directions and speeds) were collected by an RD Instruments (San Diego, California) acoustic Doppler current profiler (ADCP) aboard the "Townsend Cromwell". Depth-temperature profiles were collected by a Sippican Ocean Systems (Marion, Massachusetts) expendable bathythermograph (XBT) recorder aboard the "Townsend Cromwell". XBT probes were launched approximately every 6 h during a track.

Aggregate depth and temperature distributions were calculated based on 10 m and 1C° bins, respectively (Holland et al. 1990 a, b). These data were expressed as a fraction of the total track time for each fish, and the bins were averaged across all fish. Aggregate temperature distributions also were calculated, where by temperatures are expressed relative to the mixed-layer temperature.

## Results

Estimated body weights, calculated fork lengths, and the duration of the tracks of *Tetrapturus audax* are given in Table 1. Fish 4 apparently died after 4 h, although it had appeared healthy upon release. Its rate of descent (≅10 m $\text{min}^{-1}$) was clearly that of a dead or dying fish, and was far slower than that of a shed transmitter (≅ 30 m $\text{min}^{-1}$, Holland et al. 1990 b). All data from Fish 4 have been omitted. No other marlin succumbed nor shed its transmitter whilst being tracked. All fish, except Fish 6, were followed until they were lost in deteriorating sea conditions: the fish were at the surface and the choppy seas and large swells significantly reduced the range over which the transmitter could be heard. Fish 6 had to be abandoned after 51 h because of lack of ship time.

### Vertical movements and temperature

Vertical movements of the marlin and the simultaneously gathered depth-temperature data are shown in Fig. 1. It is apparent from this figure that striped marlin in Hawaiian waters spend the majority of their time either in, or immediately below, the mixed layer. The fish do make brief excursions into water as cold as 18 °C, but no signif-

**Table 1.** *Tetrapturus audax*. Estimated body weight, calculated fork length, and duration and dates of tracks for six striped marlin equipped with ultrasonic transmitters. Fork lengths were calculated from estimated body weights using weight–length regression equation given in Skillman and Yong (1974)

| Fish No. | Estimated wt (kg) | Fork length (cm) | Duration of track (h) | Date of track |
|---|---|---|---|---|
| 1 | 37 | 210 | 14 | 22–23 Nov. |
| 2 | 45 | 220 | 22 | 24–25 Nov. |
| 3 | 37 | 210 | 23 | 3–4 Dec. |
| 4 | 57 | 230 | 4 | 7 Dec. |
| 5 | 50 | 230 | 41 | 9–11 Dec. |
| 6 | 45 | 220 | 51 | 16–18 Dec. |

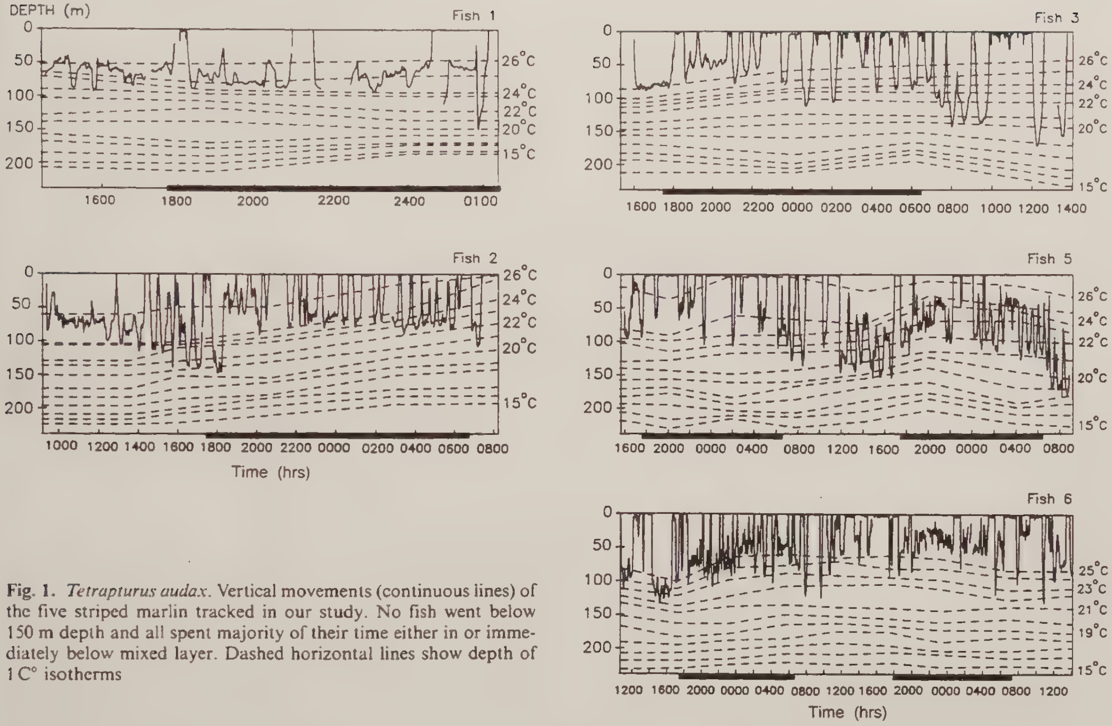

Fig. 1. *Tetrapturus audax*. Vertical movements (continuous lines) of the five striped marlin tracked in our study. No fish went below 150 m depth and all spent majority of their time either in or immediately below mixed layer. Dashed horizontal lines show depth of 1 C° isotherms

icant amount of time is spent at this temperature. Fig. 1 also shows that there are no obvious day–night differences in depth distribution, as seen in tunas (Holland et al. 1990 b).

Fig. 2 summarizes time at depth and time at temperature for all fish. The striped marlin in our study spent almost 30% of their time at depths shallower than 10 m (Fig. 2a). The second peak in the time at depth distribution (51 to 90 m, Fig. 2a) reflects the approximate depth of the bottom of the mixed layer. Fig. 2b shows the time spent at various absolute temperatures and Fig. 2c the time spent at temperatures relative to the mixed-layer temperature. Both (b) and (c) reveal that striped marlin spend >85% of their time either within, or immediately below, the mixed layer.

## Horizontal movements

### *Fish 1*

Fish 1 was captured ≅ 8 nautical miles (15 km) northwest of Keahole Point (Fig. 3) and was released at 11.07 hrs. Because of equipment failure, neither depth nor positional data (except the point of capture) were obtained until 13.00 hrs. The GPS satellite was not transmitting during the majority of the track, so oceanic current information was not obtained. (The ADCP requires real-time data on ship position and speed provided by the GPS receiver). Also, accurate positional information was unobtainable between 18.00 and 22.00 hrs because the GPS satellite was not transmitting and the data from the other navigational systems were unreliable.

Fish 1 moved north, both day and night (Fig. 3), until contact was lost at ≅01.00 hrs in rough water near the edge of the Alenuihaha Channel. The fish had an average ground speed of 2.0 knots (1.0 m s$^{-1}$).

The Alenuihaha Channel is noted for its difficult sea conditions, because the trade winds are funneled between the islands of Hawaii and Maui (the island immediately to the north). Because Fish 1 moved rapidly north into the channel, all subsequent fishing efforts were moved ≅ 20 to 25 nautical miles (37 to 46 km) south.

### *Fish 2*

Fish 2 was released at 09.26 hrs at a point ≅12 nautical miles (22 km) southwest of Keahole Point. It moved south for about 20 min, then turned and headed north for the remainder of the track (Fig. 3). Contact was lost at around 07.30 hrs the following morning in rough sea conditions [≅1 to 2 m swells and 20 to 25 knot (10 to 13 m s$^{-1}$) wind]. The marlin was briefly relocated at 09.05 hrs and then immediately lost again. The fish's course paralleled that of Fish 1 for the entire track. Oceanic current data were not obtained because the GPS satellite was again transmitting only intermittently.

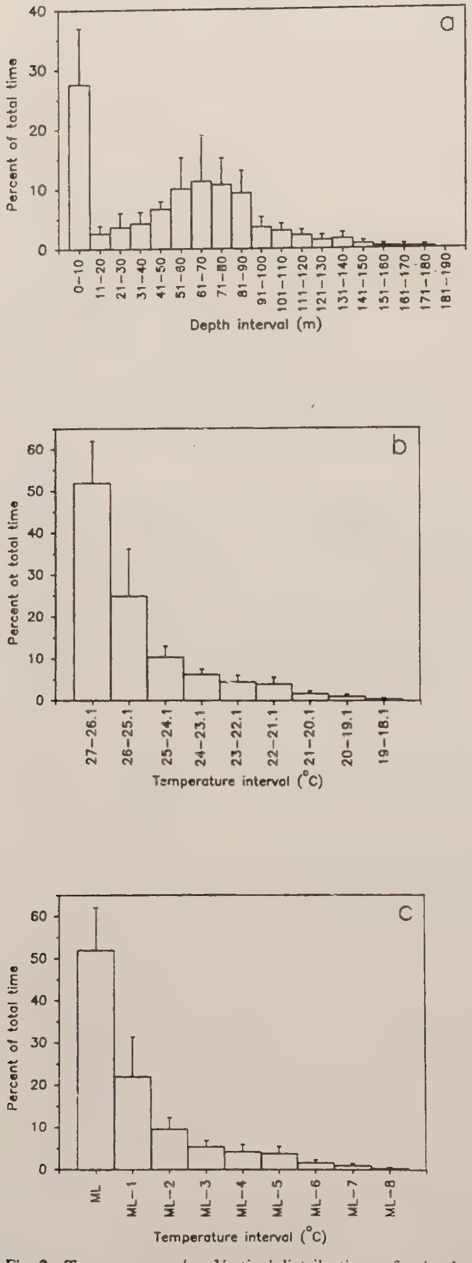

Fig. 2. *Tetrapturus audax*. Vertical distributions of striped marlin in Hawaiian waters expressed as percent time (mean ± standard error of mean) spent at a specific depth (a), at a specific temperature (b), and at temperatures relative to mixed-layer (ML) temperature (c). In (c), ML-1 represents water temperature 1 C° below mixed-layer temperature, ML-2 water temperature 2 C° below mixed-layer temperature, etc. Data confirm that striped marlin spend most of their time in or immediately below mixed layer (i.e., the warmest water available). Maximum depths reached by striped marlin appear to be limited by temperatures that are 8 C° below (ML-8) mixed-layer temperature

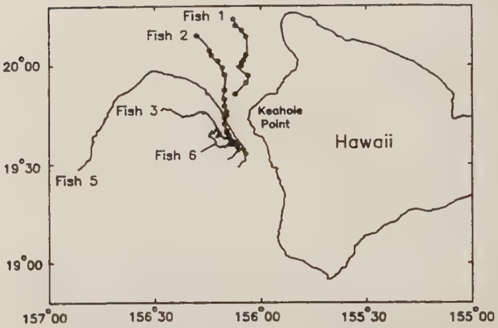

Fig. 3. *Tetrapturus audax*. Island of Hawaii and movements of five striped marlin. Distance scale for fish movements in this and subsequent figures is represented by longitude (1 min of longitude = 1 nautical mile = 1.852 km), with circles indicating hourly positions. Hourly positions have been omitted from tracks of Fish 3, 5, and 6 for legibility

### *Fish 3*

Fish 3 was released at 15.59 hrs in approximately the same area as Fish 2 (Fig. 3). It proceeded north for 2 h, then turned to a more northwesterly heading until first light the following morning (07.00 hrs), when it changed to an almost due westerly course (Fig. 4a). Most (but not all) of the horizontal movements of Fish 3 appear to be due to the prevailing currents (cf. Fig. 4a and b). After $\sim$18.00 hrs (2 h after release), the fish seemed to attempt to maintain a westerly heading but was pushed onto a northwesterly course by the current. The fish's speed over ground at this time was 1.8 knots (0.93 m $s^{-1}$). When the fish reached an area where the currents were more westerly (at ≅07.00 hrs), its speed over ground increased to 3.9 knots (2.0 m $s^{-1}$), presumably because the fish's intended heading and the current were almost parallel.

### *Fish 5*

Fish 5 was released at 16.00 hrs in approximately the same area as Fish 2 and 3 (Fig. 3). This marlin moved northwest for the first night, then gradually turned west and then southwest over the next day. It finally assumed an almost due-south heading during the second night and next morning (Fig. 5a). Average speed over ground for the first 37 h of the track from (16.00 to 07.00 hrs, Fig. 5a) was 2.0 knots (1.0 m $s^{-1}$). The overall displacement of this fish appears to have been caused by currents, since its course parallels the direction of the currents until approximately dawn (07.00 hrs) on the second day (Fig. 5b). The fish may have been attempting to maintain a due westerly course after dawn on the second day, but was pushed to a southwesterly course by the strong (4.2. knots, 2.2 m $s^{-1}$) southerly current.

### *Fish 6*

Fish 6 was released (at 10.42 hrs in roughly the same place as Fish 3 and 5 (Fig. 3). For the first 24 h, the

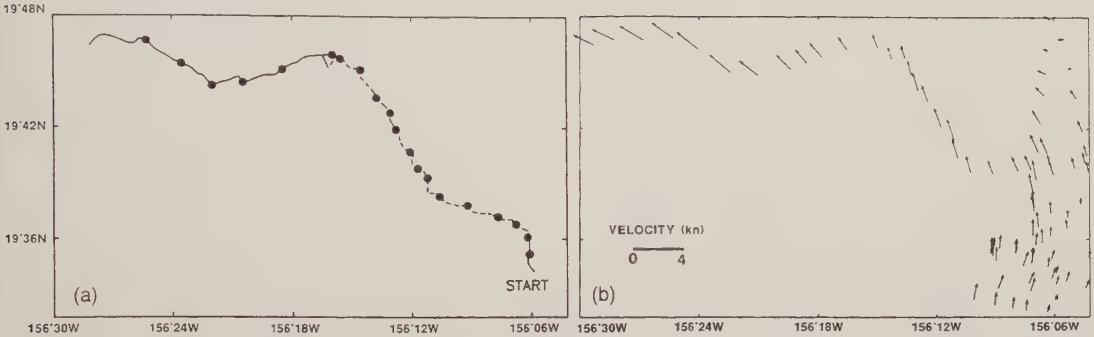

**Fig. 4.** *Tetrapturus audax*. Horizontal movements of Fish 3 (a) and simultaneously gathered oceanic current data (b). Current data are for 20 to 40 m depth, i.e., shallowest depth range from which reliable data can be obtained by acoustic Doppler current profiler. For current speed, 4 knot scale-line = 2.06 m $s^{-1}$. Here and in Figs. 5 and 6, continuous portion of trace indicates daylight movements and dashed portion nighttime movements

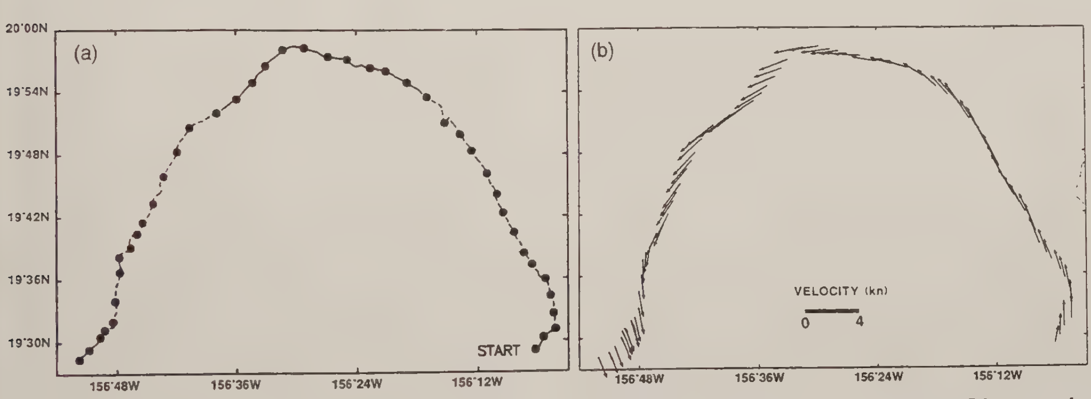

**Fig. 5.** *Tetrapturus audax*. Horizontal movements of Fish 5 (a) and simultaneously gathered current data (b). Fish's movements appeared to be strongly influenced by current direction for most (37 h) of track. During last 5 h (07.00 to 11.00 hrs), fish appeared to attempt to hold a westerly course, but was pushed to southwest by a strong (4.2 knots, 2.2 m $s^{-1}$) southerly current

"Kaahele'ale" followed the marlin while the "Townsend Cromwell" mapped the local current field. The fish moved in a looping pattern (Fig. 6a), so that it remained in the same area rather than moving off as the other marlin had done. Unlike the other fish, the movements of Fish 6 appear to be almost totally uninfluenced by the northerly-directed current (Fig. 6b). Its speed over ground, however, was strongly influenced by the current. When moving nearly parallel with the current (from the start of the track until ≅ 14.30 hrs), ground speed was about 2.1 knots (1.1 m $s^{-1}$). When clearly moving against the current (from ≅14.30 to 18.00 hrs), its ground speed was considerably slower (0.7 knots, 0.36 m $s^{-1}$).

## Discussion

The depth preferences of the *Tetrapturus audax* in our study are similar, but not identical, to those of striped marlin tracked off California by Holts and Bedford (1990). During both studies, the fish spent a significant amount of time in the upper 10 m. Three of the eight fish tracked by Holts and Bedford did not descend below 40 m, and the deepest dive was 93 m. The deepest descent observed during our study was ≅170 m, and our fish spent ≅40% of their time between 51 and 90 m. Our results are consistent with those of Boggs (1992), who found the catch rates of striped marlin near the Hawaiian Islands to be highest for longline hook fishing between 40 and 120 m.

It seems likely that the depth distribution of striped marlin is strongly influenced by water temperature rather than by an absolute depth preference. Comparison of our data with those of Holts and Bedford (1990), reveals that striped marlin do not have an absolute temperature preference. The fish we followed spent ≅80% of their time between 25.1 and 27 °C, and never ventured in water colder than 18 °C. In contrast, because of the lower mixed-layer temperature, the striped marlin tracked off California spent the majority of their time between 20

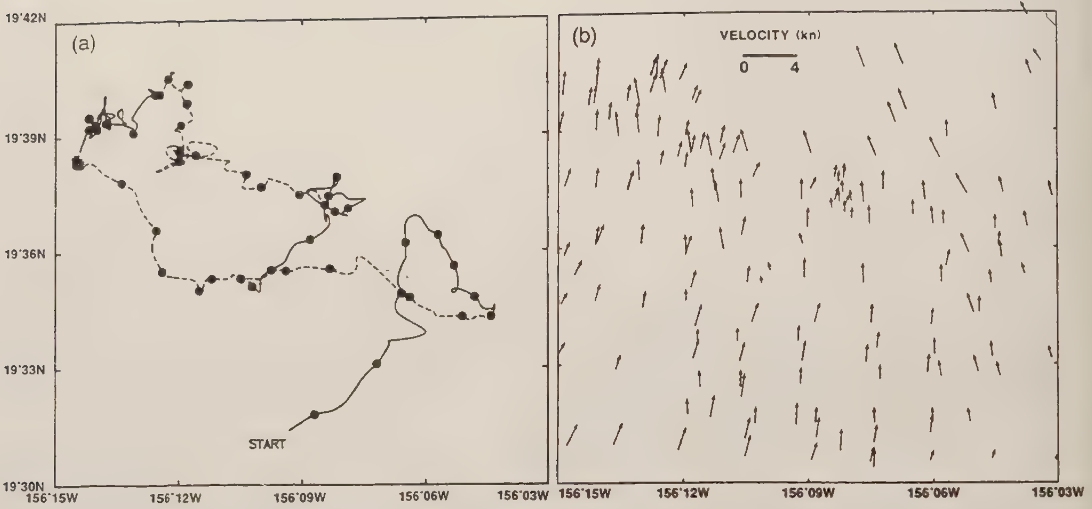

**Fig. 6.** *Tetrapturus audax*. Horizontal movements of Fish 6 (a) and simultaneously gathered current data (b). Unlike other striped marlin tracked during our study, and despite a relatively strong (≈2.5 knots, 1.3 m s$^{-1}$) northerly current, fish remained in relatively small area by moving in looping pattern

and 21 °C, and regularly penetrated into waters of 14 °C, or even 12 °C. When temperature is expressed relative to the mixed layer (Fig. 2c), however, the distributions appears to be the same for both groups. Striped marlin near the Hawaiian Islands and near California both spent the vast majority of their time either in the mixed layer or in water no colder than 2 C° below that of the mixed layer. No fish in either study descended into waters that were more than 8 C° colder than the temperature of the mixed layer. This similarity in behavior occurred in spite of the fact that the fish tracked by Holts and Bedford were somewhat larger (50 to 80 kg) than the fish tracked in our study (37 to 57 kg). In brief, striped marlin appear to spend the majority of their time at the highest water temperature available, and water temperature more than 8 C° below mixed layer temperature forms the floor of the striped marlin habitat. It is the change in water temperature (relative to mixed-layer temperature), rather than absolute temperature, that limits striped marlin vertical movements.

The horizontal displacements of striped marlin off California (Holts and Bedford 1990) and those near the Hawaiian Islands also appear strikingly similar. In both studies, most fish moved in relatively straight lines or slowly curving arcs. Similar horizontal displacements have been observed in Indo-Pacific blue marlin in Hawaiian waters (Yuen et al. 1974, Holland et al. 1990a, Block et al. 1992a). Although oceanic current data were not collected simultaneously in these studies, the paths of Indo-Pacific blue marlin appear to follow the probable cyclonic and anticyclonic eddy patterns (Robinson and Lobel 1985, Lobel and Robinson 1986) which occur on the leeward side of the Island of Hawaii where the fish were tracked.

Relatively straight-line movement is not universal, however. Of the eight striped marlin tracked for 20 h or more by Holts and Bedford (1990), three followed looping courses that kept them in the areas where they were originally caught. Of the five fish tracked in our study, four left the areas where they were caught, and one did not. Because of the overall similarity of the vertical movements in all striped marlin tracked to date, the differences in horizontal movement patterns are probably not due to differences in the extent of injuries acquired during capture. Indeed, Fish 4, the individual that died 4 h after capture, spent the entire time within a few meters of the surface. This appears to be a behavior pattern indicative of badly injured fish. An almost identical situation was observed by Block et al. (1992a). In their study, the one Indo-Pacific blue marlin that was confirmed to have been killed by a shark also spent the entire tracking period (15 h) immediately below the surface, and never ventured deeper than ≅30 m.

The relatively straight-line movement patterns of striped and Indo-Pacific blue marlin contrast sharply with those of skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna, and bigeye tuna tracked near the Hawaiian Islands (Yuen 1970, Holland et al. 1990b). The tunas showed a strong 24 h rhythm in their behaviors. They repeatedly returned to the same areas at the same time for several days, and often returned via different routes. It appears unlikely, therefore, that tuna movements are significantly affected by currents. The reasons for the dramatic differences in the behaviors of tunas and marlins remain unexplained and should be investigated, particularly because tunas are major prey items (in terms of weight) of Indo-Pacific blue and striped marlin (Baker 1966, Brock 1984).

Because our data clearly show that striped marlin movements can be strongly influenced by oceanic currents, we suspect that in studies showing relatively straight-line movements of Indo-Pacific blue and striped marlin (Holland et al. 1990a, Holts and Bedford 1990, Block et al. 1992a, b), some fraction of the overall horizontal displacements of the tracked fish were due to currents. Similar influences of currents on the movements of blue sharks have been observed by Carey and Scharold (1990). Comparisons of "swimming speeds" between studies that do not-telemeter this parameter directly are, therefore, problematic. Note, however, that ground speeds (≅ 1 to 2 knots) of Indo-Pacific blue and striped marlin are remarkably similar whether observed by acoustic telemetry (Holland et al. 1990b, Holts and Bedford 1990, Block et al. 1992b, and present study) or by release and recapture of tagged individuals (Squire 1987). The similarity of these data may reflect either common oceanic current velocities (Lobel and Robinson 1986), common swimming speeds or, most likely, a combination of the two.

Because of the imprecision of estimating geographical position and distances from the tracking vessel to the fish, a zig-zag pattern of fish movement is not really detectable. If fish movement is indeed highly irregular, ground speeds calculated from the tracking vessel's position may underestimate sustainable swimming speeds. In the one study that directly telemetered swimming speeds of Indo-Pacific blue marlin (Block et al. 1992b), the fish swam slower then 2 knots ($1.0 \mathrm{~m~s}^{-1}$) for 93% of the time. Bursts of high speeds, up to 3.6 knots ($1.8 \mathrm{~m~s}^{-1}$), lasted $<1$ min. When not in currents, ground speeds of blue sharks approximated measured swimming speeds, indicating that both Indo-Pacific blue marlin and blue sharks do not dart about (Carey and Scharold 1990, Carey unpublished observations) It seems likely that the same is true for striped marlin.

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**Abstract.**–Developmental stages of pygmy poacher, *Odontopyxis trispinosa*, and blacktip poacher, *Xeneretmus latifrons*, are described and illustrated from specimens collected from the northeastern Pacific Ocean. External morphology, pigmentation, and meristic features are described which distinguish larvae of these species from other agonids occurring in these waters.

Postanal pigment patterns, particularly on the caudal finfold, distinguish preflexion larvae. *Odontopyxis trispinosa* larvae possess a semicircular patch of melanophores that covers nearly the entire caudal finfold. The caudal finfold of preflexion *X. latifrons* larvae are void of pigment with the exception of a small patch of melanophores near the ventral margin of the notochord tip. Flexion and postflexion larvae can be distinguished by caudal and anal fin pigmentation, head spination, and adult meristic features.

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# Development of larval and early juvenile pygmy poacher, *Odontopyxis trispinosa*, and blacktip poacher, *Xeneretmus latifrons* (Scorpaeniformes: Agonidae)

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The family Agonidae is a morphologically diverse group of relatively small, benthic marine fishes. Agonids, commonly called poachers, are characterized by the presence of fused or overlapping bony plates that encase the body. Fifteen genera represented by 25 species occur in the northeastern Pacific (Matarese et al., 1989).

The pygmy poacher *Odontopyxis trispinosa* is a small (to 8.1 cm SL) subtidal agonid distinguished by an elongate body, small vertical spine at the snout tip, and a moderately developed occipital pit divided by a longitudinal ridge. Fin-element counts of *O. trispinosa* are D III-VI, 5-7; A 5-7; P 13-15; V I,2 (Matarese et al., 1989). The blacktip poacher *Xeneretmus latifrons* is a larger (to 19 cm SL) subtidal agonid distinguished by black margins on the dorsal fins and a weakly developed occipital depression (Miller and Lea, 1972; Hart, 1973). Fin-element counts of *X. latifrons* are D VI-VIII, 6-8; A 6-9; P 13-15; V I,2 (Matarese et al., 1989). The presence of spiny scales on the eyeballs distinguishes *X. latifrons* from *X. leiops*. The absence of cheekplates distinguishes *X. latifrons* from *X. triacanthus* (Miller and Lea, 1972; Eschmeyer et al., 1983).

Freeman (1951) hypothesized that these two taxa are closely related phylogenetically and placed them in his subfamily Xeneretminae. The cladistic analysis of Kanayama (1991) demonstrated close relationships between the two taxa which he placed in the subfamily Anoplagoninae.

The geographic range of adult *O. trispinosa* extends from Southeast Alaska to central Baja California. Adult *X. latifrons* occur over a slightly narrower range from Vancouver Island to northern Baja California (Eschmeyer et al., 1983). Both taxa occur at depths of 18–370 m (Miller and Lea, 1972; Hart, 1973). Larval *O. trispinosa* and *X. latifrons* are the most commonly occurring agonids in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton collection[1].

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[1] Moser, H. G., ed. Guide to the early stages of fishes from the California Current region. Southwest Fisheries Science Center, NMFS, P.O. Box 271, La Jolla, CA 92038. In preparation.

Larval development of agonids is poorly known. Washington et al. (1984) and Maeda and Amaoka (1988) reported that formation of most external body parts, including dermal bony plates and spines, begins early in larval development.

Development of the pygmy poacher (*O. trispinosa*) is described for the first time here. Development of *X. latifrons* is clarified based on new material. A partial developmental series (7, 10, 16 mm SL) of *X. latifrons* was previously described by Marliave (1975). Washington et al. (1984) included a single illustration of *X. latifrons* (9.6 mm SL) which differed markedly in appearance from those in Marliave (1975). Matarese et al. (1989) combined the illustrations from both sources to create a complete developmental series. As a result, some confusion exists as to which illustrations in this series are actually those of *X. latifrons* larvae. The following descriptions are the first complete accounts of larval development in the family Agonidae. Characters are presented that permit identification of these larvae from field collections.

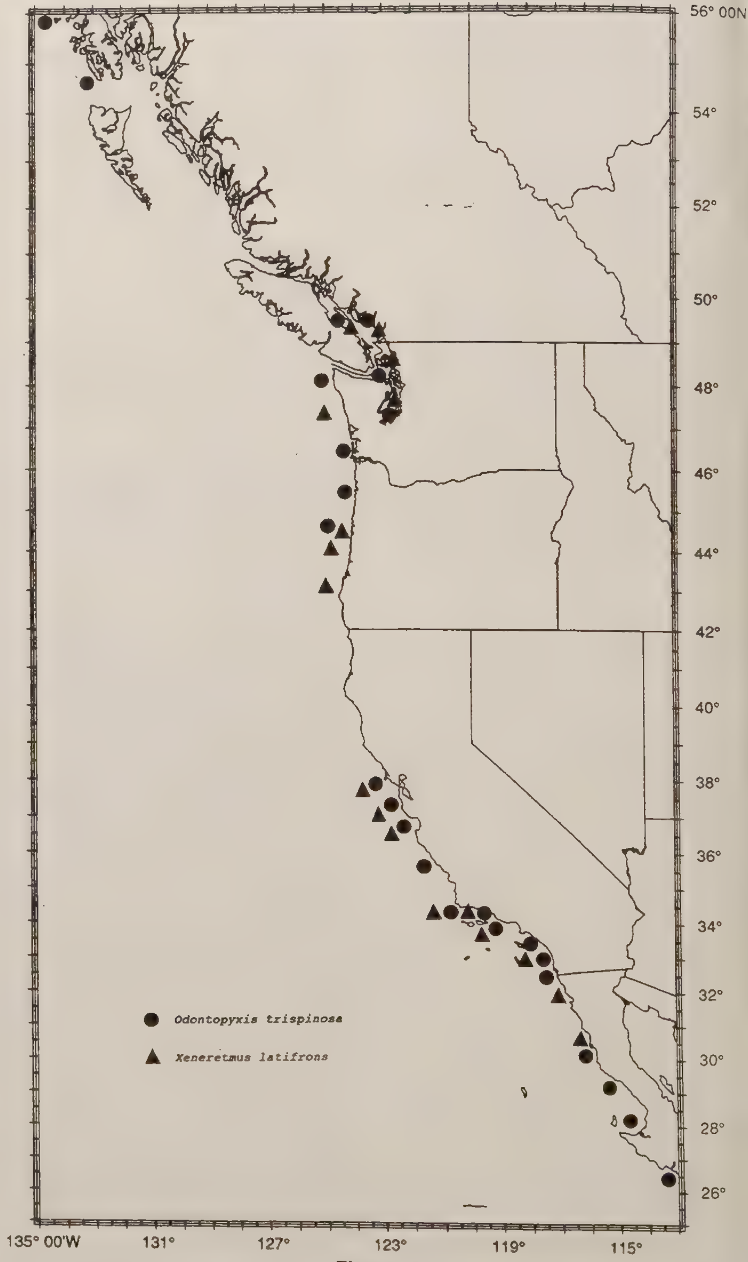

Figure 1

Collection locations of *Odontopyxis trispinosa* and *Xeneretmus latifrons* larvae and early juveniles used in this study.

## Methods

### Specimens

Agonid larvae examined in this study were obtained from collections made off the coasts of Baja California, California, Oregon, Washington (including Puget Sound), Southeast Alaska, and the inside passage waters of British Columbia, Canada (Fig. 1). One hundred and thirty-six *O. trispinosa* (4.3–56.0 mm SL) and 77 *X. latifrons* (4.8–79.0 mm SL) were examined. The largest specimens of each taxa were determined to be adults and are not included in the descriptions. Larvae and juveniles of both taxa were collected with dipnets, 60- and 70-cm bongo nets, Isaacs-Kidd midwater trawls, Tucker trawls, sled trawls, and bottom trawls. Collections were made by the Vancouver Public Aquarium (VPA), Oregon State University (OSU), University of Washington (UW), NOAA's Southwest Fisheries Science Center (SWFSC-CalCOFI program), and the Alaska Fisheries Science Center (AFSC) from the years 1932 to 1991. Specimens are currently housed in the larval fish collections of these institutions. Larvae and juveniles were originally fixed in 3.5 or 5.0% formalin and subsequently transferred and stored in 3.5% buffered formalin or 70% ethanol.

Larvae of *O. trispinosa* and *X. latifrons* were identified using the serial approach. This method uses adult characters to progressively link juveniles to smaller specimens through a continuous sequence of shared similarities. Pigmentation, head spination, body morphology, dermal plates, and meristic features were all used as diagnostic characters. Identification of adult and juvenile specimens was accomplished by using methods of Miller and Lea (1972), Hart (1973), and Kanayama (1991). Nomenclature and taxonomic classification of the family Agonidae follow Kanayama (1991). Developmental series were illustrated by using a camera lucida attached to a dissecting stereomicroscope.

Only melanistic pigmentation is described because formalin fails to preserve color pigments. In the description of pigmentation, the term "band" refers to any aggregation of melanophores that approximates a vertically oriented rectangle. A "bar" also approximates a rectangle but is horizontally oriented. A "patch" is any other distinguishable aggregation of melanophores.

## Measurements

The following measurements were made on 45 larvae and early juveniles of *O. trispinosa* and 45 larvae of *X. latifrons* by using an ocular micrometer in a stereomicroscope:

**Standard length (SL)**—Snout tip to notochord tip prior to development of caudal fin, then to posterior margin of hypural element. (All body lengths in this study are standard lengths.)

**Body depth**—Vertical distance from dorsal to ventral body margin at pectoral-fin base.

**Snout to anus length**—Distance along body midline from snout tip to a vertical line through center of anal opening.

**Head length (HL)**—Snout tip to posterior edge of opercle (to pectoral-fin base in small larvae before opercular margin is visible).

**Head width**—Distance across head between dorsal margins of orbits.

**Snout length**—Snout tip to anterior margin of orbit of left eye.

**Eye diameter**—Greatest diameter of left orbit.

**Pectoral fin length**—Distance from pectoral-fin base to tip of the longest ray.

## Osteology

Selected specimens were cleared and differentially stained to identify cartilage and bone with alcian blue and alizarin red-S (Pothoff, 1984). Skeletal elements and dermal plates were recognized as ossified upon initial uptake of alizarin red-S. Twenty-seven *O. trispinosa* (5.3–41 mm) and 12 *X. latifrons* (7.4–39.2 mm) were cleared and stained for study. Counts of meristic features were made on stained specimens only. Not all stages of development were stained for *X. latifrons* because specimens were limited. Preflexion, flexion, and postflexion stage larvae were stained (Kendall et al., 1984). Nomenclature of skeletal elements follows that used by Leipertz (1985) for *X. triacanthus*. Plate nomenclature follows that of Gruchy (1969) and is described in Figure 2. Terminology of larval head spination follows that proposed for adult

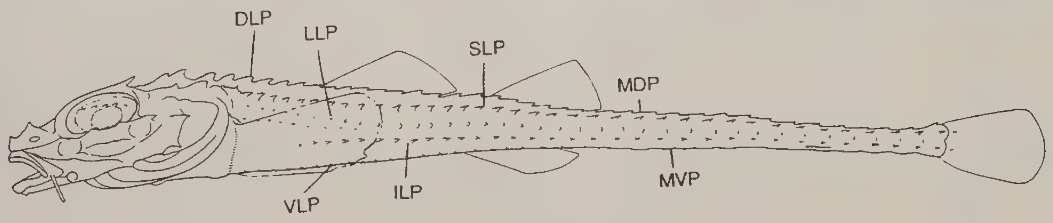

**Figure 2**

Terminology of bony plates in agonid larvae: DLP=dorsolateral; MDP=mid-dorsal; SLP=supralateral; LLP=lateral line; ILP=infralateral; VLP=ventrolateral; MVP=mid-ventral (after Gruchy, 1969).

agonids by Laroche (1986). For larvae with spines and no named analogous adult spine, terminology follows Moser and Ahlstrom (1978) or Richardson and Laroche (1979) for larvae of rockfish *Sebastes* spp. (another Scorpaeniform) (Table 1, Figs. 3 and 4).

## Results

### Development of *Odontopyxis trispinoa*

**Morphology** Larvae of *O. trispinosa* are elongate and slender with mean body depth at the pectoral fin origin of 11.7% SL in preflexion specimens decreasing to 10.7% SL in flexion and postflexion larvae (Tables 2 and 3). Mean head length is 18.4% SL in preflexion larvae and increases to 23.8% SL in juveniles (Table 3). Mean head width is approximately 50.0% HL throughout larval development and decreases to 37.1% HL in juveniles (Table 3). Mean snout length increases from 20.4% HL in preflexion larvae to 27.0% HL in postflexion larvae and eye diameter decreases from 33.3% HL in preflexion larvae to 23.3% HL in juveniles. Mean pectoral-fin length increases from 7.0% SL in preflexion larvae to 19.5% SL in postflexion larvae (Table 3). The gut is moderately long: mean snout to anus distance is 47.9% SL in preflexion larvae and decreases to 33.0% SL in juveniles.

**Pigmentation** Pigmentation in *O. trispinosa* larvae was relatively consistent among specimens and is a useful distinguishing character (Fig. 5).

**Head region** Pigmentation on the head of preflexion larvae is present as rows of melanophores on the upper and lower jaws. A few additional melanophores are present on the snout. Melanophores on the opercular and hyoid regions join the upper and lower jaw pigmentation to form a continuous swath giving larvae a "bearded" appearance (Fig. 5A). In flexion larvae, additional melanophores appear posterior to the eye.

**Lateral body and gut region** The dorsolateral surface of the body above the gut is covered with melanophores with the exception of a patch along the dorsal midline above the pectoral fin. The dorsolateral pigmentation recedes ventrolaterally toward the gut with development and is completely absent in postflexion larvae. Melanophores cover nearly the entire caudal portion of the body in preflexion larvae. In some specimens, the notochord tip is unpigmented. In late flexion and postflexion larvae, pigmentation on the lateral body surface begins to separate gradually into seven bands (Fig. 5D). The first band extends from the posterior region of the first dorsal fin to the ventral body midline immediately posterior to the anus. The second band extends between the first two soft rays of the

**Table 1**

Head spine terminology in agonid larvae listed by sequence of development in *Odontopyxis trispinosa*. (P) designates dermal plate.

| Abbreviation | Spine/Plate name | Bone of origin | Adult spine/plate |
|---|---|---|---|
| PA | Parietal | Parietal | Parietal |
| SPO | Supraocular | Frontal | Supraocular |
| SC | Supracleithral | Supracleithrum | Supracleithral |
| CO | Coronal | Frontal | (Overgrown) |
| PT | Pterotic | Pterotic | Pterotic |
| NA | Nasal | Nasal | Nasal |
| APO-4 | 4th Anterior Preopercular | Preopercle | (Overgrown) |
| PPO-1,2 | 1st, 2nd Posterior Preopercular | Preopercle | Preopercular |
| PPO-3,4 | 3rd, 4th Posterior Preopercular | Preopercle | Preopercular |
| SIO-5,6 | 5th, 6th Superior Infraorbital | Infraorbital 3 | Posterior infraorbitals |
| CL | Cleithral | Cleithrum | (Overgrown) |
| TM | Tympanic | Frontal | (Overgrown) |
| OP | Opercular | Opercle | Opercular |
| FR | Frontal | Frontal | (Overgrown) |
| SOP | Subopercular | Subopercle | Gill Cover Spine |
| SIO-1,2 | 1st, 2nd Superior Infraorbital | Infraorbital 1 (Lachrymal) | Anterior Infraorbital |
| PSO-1 | 1st Postocular | Frontal | Postocular |
| PSO-2,3 | 2nd, 3rd Postocular (P) | (Dermal) | Postocular Plates |
| RO | Rostral | Rostral Plate | Rostral |
| PST | Posttemporal (P) | (Dermal) | (Overgrown) |
| IIO-1,2 | 1st, 2nd Inferior Infraorbital (P) | (Dermal) | Anterior, Medial Cheek Plates |
| SIO-3,4 | 3rd, 4th Superior Infraorbital | Infraorbital 2 (Jugal) | Medial Infraorbital |
| IIO-3 | 3rd Inferior Infraorbital (P) | (Dermal) | Posterior Cheek Plate |
| SCL | Sclerotics (P) | Sclerotic | Eyeball Plates |

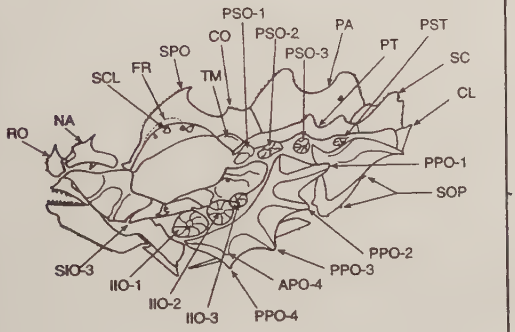

**Figure 3**

Positions and abbreviations of larval head spines and plates in agonids. Based on a 17.2-mm stained larva of *Odontopyxis trispinosa* (modified from Moser and Ahlstrom (1978), Richardson and Laroche (1979), and Laroche (1986)).

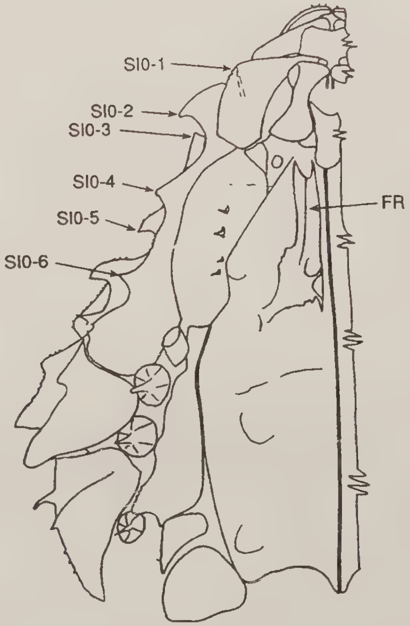

**Figure 4**

Top view above eye showing superior infraorbital and frontal spines of a 17.2-mm SL, cleared and stained *Odontopyxis trispinosa*.

dorsal and anal fins and is connected ventrally to the first band by a bar. The third band extends from the posterior half of the second dorsal fin to the posterior half of the anal fin. The remaining four bands are evenly spaced on the body between the posterior edges of the second dorsal and anal fins and the caudal fin. The third, fifth, and seventh bands are the widest. The posteriormost band of pigmentation in postflexion larvae and early juveniles is located at the hypural margin and is continuous with the caudal-fin pigment.

The entire ventral and lateral surfaces of the gut in preflexion larvae are covered with pigmentation. A dense row of melanophores is present along the ventral midline from the isthmus to the end of the preanal finfold. The ventral midline pigmentation can be distinguished easily in lateral view through the postflexion stage. In some specimens, a small, circular, unpigmented area is present on the lateral surface of the gut posterior to the pectoral-fin rays.

**Fins** The base of the pectoral fin is completely covered with melanophores throughout development. Pigmentation is absent from the pectoral-fin blade, rays, and membrane.

Most preflexion and flexion specimens possess a small group of melanophores on the anterior portion of the dorsal finfold near the body margin over the gut (Fig. 5A). This patch migrates posteriorly with development and becomes the pigmentation seen on the first dorsal fin in postflexion larvae and juveniles (Fig. 5, C and D). A larger patch of melanophores is present at approximately midbody which usually extends to the dorsal edge of the finfold in preflexion larvae. This dorsal midbody patch recedes toward the body and splits into two somewhat triangular-shaped patches of pigmentation in flexion larvae. This larger patch of pigmentation is retained on the second dorsal fin in postflexion larvae and juveniles. The finfold patches roughly correspond to body bands on postflexion and juvenile specimens. Three additional triangular-shaped patches of melanophores are present approximately two-thirds of the distance between the anus and notochord tip on the dorsal finfold and form a continuous region of pigment extending to the caudal finfold. The triangular-shaped patches of pigmentation separate in flexion larvae and disappear as the finfold recedes in postflexion larvae.

### Table 2

Morphometric measurements (in millimeters) of 45 *Odontopyxis trispinosa* larvae and early juveniles. Specimens between dashed lines (— —) were undergoing notochord flexion.

| Standard length | Body depth | Snout to anus length | Head length | Head width | Snout length | Eye diameter | Pectoral fin length |
|---|---|---|---|---|---|---|---|
| 4.3 | 0.44 | 2.02 | 0.78 | 0.40 | 0.14 | 0.28 | 0.30 |
| 4.5 | 0.60 | 2.06 | 0.72 | 0.52 | 0.12 | 0.30 | 0.30 |
| 4.6 | 0.60 | 2.24 | 0.80 | 0.44 | 0.18 | 0.30 | 0.34 |
| 5.2 | 0.62 | 2.48 | 1.02 | 0.48 | 0.22 | 0.32 | 0.34 |
| 5.3 | 0.60 | 2.52 | 0.96 | 0.46 | 0.20 | 0.32 | 0.44 |
| 5.3 | 0.64 | 2.60 | 1.02 | 0.46 | 0.18 | 0.36 | 0.36 |
| 5.9 | 0.62 | 2.72 | 1.04 | 0.42 | 0.20 | 0.34 | 0.38 |
| 6.4 | 0.74 | 3.24 | 1.14 | 0.44 | 0.26 | 0.36 | 0.34 |
| 6.7 | 0.70 | 3.24 | 1.20 | 0.56 | 0.22 | 0.40 | 0.46 |
| 6.8 | 0.76 | 3.20 | 1.26 | 0.56 | 0.30 | 0.40 | 0.50 |
| 6.8 | 0.82 | 3.12 | 1.40 | 0.62 | 0.30 | 0.36 | 0.50 |
| 7.2 | 0.86 | 3.48 | 1.36 | 0.70 | 0.30 | 0.40 | 0.52 |
| 7.1 | 0.88 | 3.60 | 1.38 | 0.70 | 0.30 | 0.40 | 0.50 |
| 7.9 | 0.66 | 3.40 | 1.34 | 0.66 | 0.32 | 0.36 | 0.60 |
| 8.5 | 0.92 | 4.12 | 1.76 | 0.80 | 0.50 | 0.44 | 0.70 |
| 9.1 | 0.96 | 4.12 | 1.50 | 0.66 | 0.38 | 0.42 | 1.00 |
| 9.8 | 1.00 | 4.60 | 2.06 | 0.92 | 0.60 | 0.52 | 1.40 |
| 10.0 | 1.06 | 4.40 | 1.70 | 1.25 | 0.41 | 0.45 | 1.05 |
| 10.8 | 1.20 | 5.00 | 2.36 | 1.08 | 0.52 | 0.60 | 1.46 |
| 11.7 | 1.36 | 5.25 | 2.52 | 1.20 | 0.60 | 0.58 | 1.64 |
| 11.8 | 1.42 | 5.50 | 2.26 | 1.24 | 0.74 | 0.56 | 2.46 |
| 11.8 | 1.44 | 5.42 | 2.80 | 1.24 | 0.76 | 0.60 | 2.26 |
| 12.5 | 1.22 | 5.67 | 2.70 | 1.20 | 0.74 | 0.60 | 2.08 |
| 12.6 | 1.32 | 5.83 | 2.80 | 1.44 | 0.86 | 0.70 | 2.48 |
| 12.7 | 1.26 | 5.42 | 2.76 | 1.28 | 0.76 | 0.64 | 2.42 |
| 12.8 | 1.30 | 5.83 | 2.70 | 1.20 | 0.68 | 0.60 | 2.42 |
| 13.7 | 1.64 | 6.33 | 2.92 | 1.50 | 0.90 | 0.72 | 2.24 |
| 13.8 | 1.58 | 6.08 | 2.92 | 1.30 | 0.80 | 0.66 | 2.35 |
| 13.9 | 1.38 | 6.08 | 3.00 | 1.46 | 0.74 | 0.70 | 2.80 |
| 14.3 | 1.50 | 6.17 | 3.25 | 1.50 | 0.80 | 0.74 | 2.96 |
| 14.7 | 1.32 | 5.87 | 3.00 | 1.40 | 0.72 | 0.76 | 2.64 |
| 14.8 | 1.52 | 6.08 | 3.00 | 1.40 | 0.76 | 0.66 | 2.68 |
| 15.0 | 1.60 | 5.83 | 3.60 | 1.54 | 0.90 | 0.84 | 3.20 |
| 15.2 | 1.70 | 5.92 | 3.84 | 1.80 | 1.00 | 0.84 | 3.20 |
| 15.4 | 1.66 | 6.17 | 3.20 | 1.60 | 0.84 | 0.72 | 3.20 |
| 15.8 | 1.62 | 6.63 | 3.50 | 1.82 | 0.91 | 0.86 | 3.16 |
| 16.7 | 1.70 | 6.50 | 4.24 | 2.04 | 1.12 | 0.98 | 3.68 |
| 17.5 | 1.87 | 6.84 | 4.26 | 1.98 | 1.13 | 0.90 | 3.08 |
| 17.7 | 2.20 | 7.58 | 4.32 | 1.86 | 1.24 | 0.84 | 3.72 |
| 17.7 | 1.76 | 7.00 | 4.48 | 2.00 | 1.20 | 1.06 | 3.68 |
| 28.0 | 2.75 | 9.58 | 7.40 | 2.88 | 1.56 | 1.64 | 4.68 |
| 32.1 | 3.33 | 10.50 | 7.58 | 2.88 | 1.84 | 1.75 | 5.58 |
| 34.8 | 3.42 | 11.30 | 8.08 | 3.12 | 1.92 | 2.00 | 6.00 |
| 36.4 | 3.92 | 11.70 | 8.25 | 2.92 | 2.17 | 1.92 | 6.33 |
| 41.6 | 4.83 | 14.50 | 9.67 | 3.33 | 2.50 | 2.25 | 6.92 |

### Table 3

Body proportions of *Odontopyxis trispinosa* larvae and early juveniles. Values given for each body proportion are expressed as percentage of standard length (SL) or head length (HL): mean, standard deviation, and range.

| Body proportion | Preflexion | Flexion | Postflexion | Juvenile |
|---|---|---|---|---|
| Sample size | 12 | 8 | 20 | 5 |
| Standard length | 5.7±1.0 (4.3–7.2) | 9.4±1.5 (7.1–11.7) | 14.5±1.9 (11.8–17.7) | 34.6±5.1 (28.0–41.6) |
| Body depth/SL | 11.7±1.0 (10.2–13.4) | 10.7±1.2 (8.4–12.4) | 10.7±0.9 (9.0–12.4) | 10.5±0.7 (9.8–11.6) |
| Snout to anus length/SL | 47.9±1.4 (45.7–50.3) | 46.2±2.5 (43.2–50.8) | 42.5±2.8 (38.9–46.6) | 33.3±1.2 (32.1–34.9) |
| Head length/SL | 18.4±1.2 (16.1–20.5) | 19.4±2.2 (16.5–21.8) | 22.4±1.9 (19.2–25.4) | 23.8±1.5 (22.7–26.4) |
| Head width/HL | 48.7±8.7 (40.4–72.2) | 50.1±9.7 (44.0–73.5) | 47.2±3.3 (43.1–54.9) | 37.1±2.0 (34.4–38.9) |
| Snout length/HL | 20.4±2.3 (16.7–23.8) | 24.8±2.7 (21.7–29.1) | 27.0±2.3 (24.0–32.7) | 24.3±2.1 (21.1–26.3) |
| Eye diameter/HL | 33.3±4.0 (25.7–41.7) | 26.1±1.9 (23.0–29.0) | 23.0±1.5 (19.4–25.3) | 23.3±0.9 (22.2–24.8) |
| Pectoral fin length/SL | 7.0±0.7 (5.3–8.4) | 10.8±2.9 (7.1–14.2) | 19.5±1.7 (16.3–21.3) | 17.1±0.4 (16.6–17.4) |

A small patch of melanophores is present on the anal finfold immediately posterior to the anus. This small patch of pigmentation is a useful character which persists until postflexion when it migrates dorsally with the receding finfold to form the bar between the first and second body bands (Fig. 5D). A large triangular-shaped patch of pigment is present at midbody and extends nearly to the finfold margin in preflexion and early flexion larvae. The large triangular-shaped patch expands ventrally to the finfold margin and becomes more rectangular shaped in late flexion larvae. This is the only pigmentation present on the anal fin in postflexion larvae and juveniles (Fig. 5, C and D). Two additional patches of melanophores are present on the anal finfold in preflexion larvae. These form a nearly continuous region of pigmentation which begins at approximately two-thirds of the distance between the anus and notochord tip which extends to the caudal finfold. This pigmentation breaks apart in late flexion larvae and disappears as the finfold recedes in postflexion larvae.

The posteriormost dorsal and anal finfold pigmentation connect and are continuous with a large semicircular patch of melanophores which covers nearly

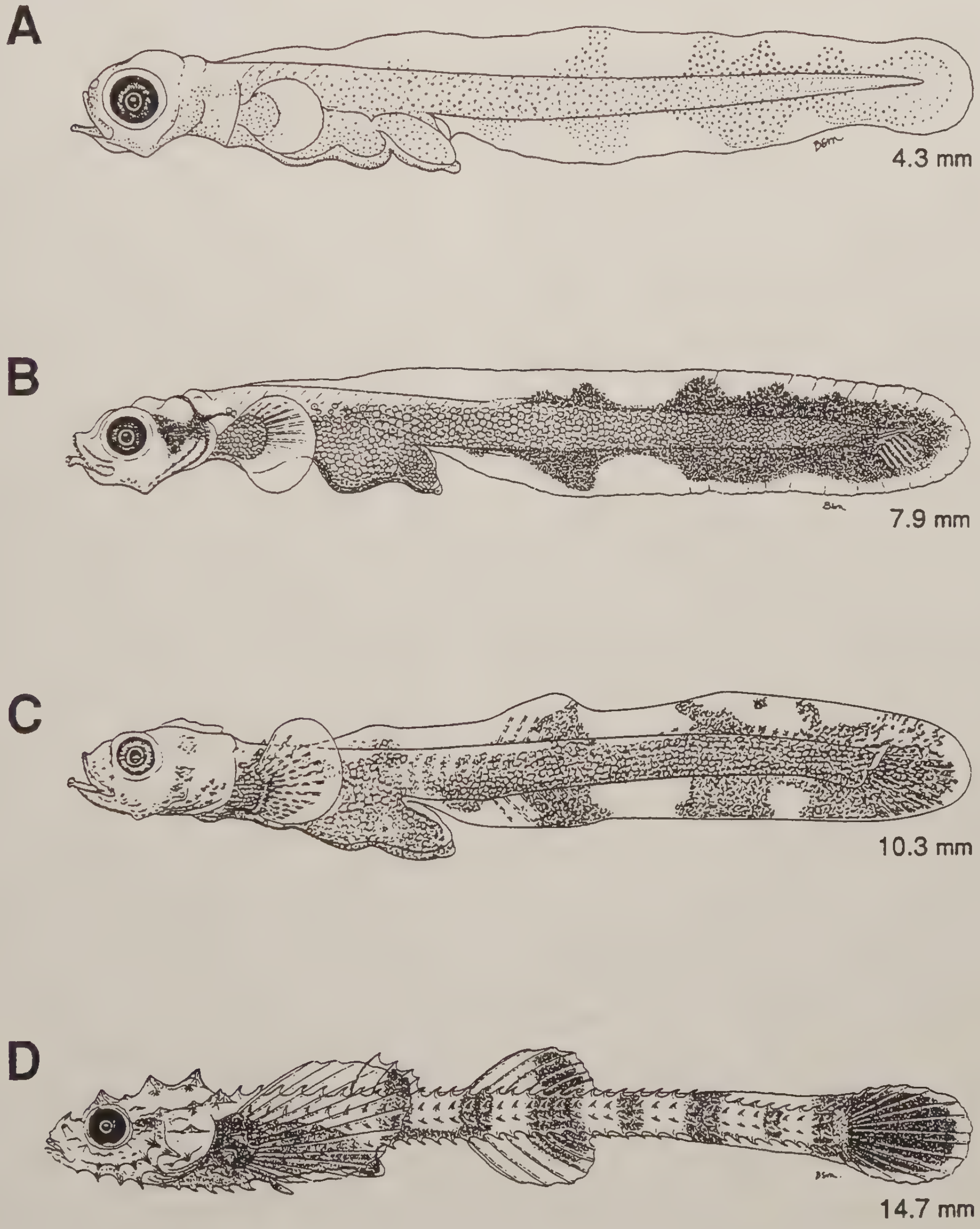

**Figure 5**

Larval stages of *Odontopyxis trispinosa*. (**A**) Preflexion larva 4.3 mm SL, CalCOFI 5405-73.50. (**B**) Early flexion larva 7.9 mm SL, CalCOFI 6304-110.32. (**C**) Flexion larva 10.3 mm SL, VPA, Lambert Channel 4/26/91 No. 7. (**D**) Postflexion larva 14.7 mm SL, CalCOFI 7412-83.44.

the entire caudal finfold. Caudal pigmentation persists throughout development.

**Osteology** Although precursors of some bony structures such as dermal plates and fin rays are discernable as early as 8.0 mm, actual ossification of skeletal elements in *O. trispinosa* does not begin until approximately 12.0 mm.

**Cranium** The parasphenoid and basioccipital bones of the cranium begin to ossify at 11.7 mm. At 13.2 mm, several bones, including the nasal, frontal, parietal, parasphenoid, basioccipital, and exoccipital are completely ossified. The rostral plate, nasal, lateral ethmoid, supraethmoid, vomer, exoccipital, lachrymal, and remainder of the circumorbital series ossify by 14.8 mm. The sphenotic, prootic, epiotic, tabular, and pterosphenoid are ossified by 27.0 mm.

**Spines** Numerous head spines are ossified at 12.6 mm including the nasal, supraocular, the large bilobed parietal, coronal, pterotics, supracleithral, anterior preoperculars and posterior preoperculars 1 and 2. The tympanic, cleithral, opercular, fifth and sixth superior infraorbital spines, and the third and fourth posterior preopercular spines are also ossified at this stage. The frontal spine forms by 13.8 mm but is not visible in lateral view because it is small and located behind the anterior margin of the supraocular spine. The frontal spine becomes overgrown with bone and is difficult to distinguish at 17.2 mm. Interopercular and superior infraorbital spines 1 and 2 begin forming at about 14.2 mm. The rostral and postocular spines and the postocular and posttemporal plates ossify at 14.8 mm. Superior infraorbital spines 3 and 4 and inferior infraorbital plates 1 and 2 are completely ossified at this size. The third inferior infraorbital and sclerotic plates are ossified by 17.2 mm. All spines described here are paired with the exception of the rostral.

**Mandibular region** The dentary, angular, and articular bones of the lower jaw are the first to ossify in postflexion larvae of 11.7 mm. At 12.6 mm, the premaxilla and maxilla are ossified.

**Palatine region** Palatine, quadrate, metapterygoid, mesopterygoid, ectopterygoid, and symplectic bones are ossified at 12.6 mm.

**Opercular region** The preopercle, opercle, interopercle, and subopercle are ossified by 12.6 mm.

**Hyoid region** The basihyal, hypohyal, urohyal, ceratohyal, epihyal, interhyal, glossohyal, and branchiostegal rays are also ossified by 12.6 mm. The hyomandibula is ossified by 27.0 mm.

**Branchial region** The pharyngobranchial teeth are the first structures to ossify by 11.7 mm. Ossification of the pharyngobranchials occurs at about 17.2 mm. The pharyngobranchials begin as four pieces of cartilage that apparently fuse before ossification of the pharyngobranchial teeth. This process, however, was not observed. The epibranchials ($n$=4) and ceratobranchials ($n$=5) also ossify by 17.2 mm. The remaining branchial support structures, including the hypobranchials ($n$=3) and basibranchials ($n$=3), ossify by 27.0 mm.

**Appendicular region** The cleithrum, postcleithrum, and coracoid are ossified by 12.6 mm. The pelvic-fin spine and all pectoral-fin rays, with the exception of the ventralmost, ossify by 12.8 mm. The two pelvic-fin rays and the final (14th) pectoral-fin ray are ossified by 13.2 mm. The supracleithrum ossifies at about 13.8 mm. At 14.8 mm, ossification of the posttemporal is completed. Ossification of the basipterygium occurs at 17.2 mm. The scapula and three radials supporting the pectoral-fin rays are ossified by 27.0 mm.

**Median fins** All dorsal- and anal-fin spines and soft rays are ossified by 12.6 mm (Table 4). Six superior principal rays and five inferior principal rays in the caudal fin are ossified at this size (total=11). One inferior principal (12), and two superior procurrent rays (13, 14) are ossified by 13.2 mm. By 17.2 mm one additional superior (15) procurrent caudal ray is formed which completes the adult count (3+6+6+0=15). Ossification of the epural, hypural plate, and pterygiophores supporting the dorsal- and anal-fin rays is completed by 27.0 mm.

**Vertebral column** Ossification of vertebral elements progresses from anterior to posterior. Notochord flexion begins at approximately 7.0 mm and is completed by 11.8 mm. All, except the posteriormost caudal vertebral centrum, are ossified by 12.6 mm. The urostyle and the anteriormost neural and haemal spines are also complete by 12.6 mm. All abdominal neural spines are complete and three additional haemal spines form anteriorly by 13.2 mm. All vertebral centra are ossified by 13.8 mm and two additional haemal spines have formed. By 14.2 mm, 22 additional haemal spines develop. All neural spines are ossified by 14.8 mm and haemal spines are complete at 15.4 mm.

**Dermal plates** Precursors of the supra (SLP) and infralateral (ILP) plates first appear as small singular spines which are distinguishable at about 8.0 mm. Ossification, however, does not begin until approximately 12.0 mm and progresses from anterior to posterior. Bone develops radially from the base of the spine to eventually form the juvenile/adult dermal plate. By 12.6 mm, ossification of the SLP and ILP series is complete. The dorsolateral and mid-dorsal (DLP+MDP) and the ventrolateral and mid-ventral (VLP+MVP) plate series are complete by 14.8 mm. The lateral line (LLP) plate series begins to form at about 14.0 mm. Lateral line plates are the only plates that begin development as bifurcate spines. Ossification of the LLP series is complete

## Table 4

Meristics of cleared and stained *Odontopyxis trispinosa* larvae and early juveniles. Specimens between dashed lines (——) were undergoing notochord flexion.

| Standard length (mm) | Dorsal fin |  | Anal fin rays | Pectoral fin rays | Pelvic fin spines, rays | Branchi-ostegal rays | Neural spines |  |  | Haemal spines | Centra |  |  | Body plates* |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | spines | rays |  |  |  |  | abdominal | caudal | total |  | abdominal | caudal | total | DLP+MDP | SLP | LLP | ILP | VLP+MVP |
| 5.3 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 5.8 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 6.1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 7.0 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 7.7 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 8.3 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 8.5 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 9.3 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 10.0 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 11.4 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 11.7 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 12.5 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 12.6 | 5 | 6 | 6 | 13 | I | 6 | 3 |  | 3 |  | 13 | 25 | 38 | 30 | 35 |  | 35 | 32 |
| 13.1 | 3 | 6 | 2 | 2 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 13.2 | 5 | 6 | 6 | 14 | I,2 | 6 | 13 | 20 | 33 | 3 | 13 | 27 | 40 | 32 | 38 | 2 | 36 | 34 |
| 13.8 |  | 3 |  |  |  | 6 | 2 |  | 2 |  |  |  |  |  |  |  |  |  |
| 13.8 | 4 | 6 | 7 | 13 | I,2 | 6 | 13 | 22 | 35 | 6 | 13 | 27 | 40 | 34 | 38 |  | 36 | 37 |
| 14.2 | 5 | 7 | 6 | 14 | I,2 | 6 | 13 | 19 | 32 | 5 | 13 | 26 | 39 | 34 | 36 | 1 | 35 | 34 |
| 14.8 | 5 | 7 | 6 | 14 | I,2 | 6 | 13 | 25 | 38 | 29 | 13 | 26 | 39 | 36 | 38 | 38 | 37 | 36 |
| 15.2 | 5 | 6 | 6 | 13 | I,2 | 6 | 13 | 25 | 38 | 23 | 13 | 26 | 39 | 37 | 39 | 33 | 37 | 37 |
| 15.2 | 4 | 4 | 6 | 14 | I,2 | 6 | 13 | 25 | 38 | 26 | 13 | 26 | 39 | 37 | 37 | 1 | 35 | 36 |
| 15.4 | 4 | 6 | 7 | 14 | I,2 | 6 | 13 | 24 | 37 | 31 | 13 | 25 | 38 | 36 | 37 | 23 | 36 | 37 |
| 16.7 | 5 | 6 | 6 | 14 | I,2 | 6 | 13 | 25 | 38 | 31 | 13 | 26 | 39 | 37 | 37 | 20 | 35 | 37 |
| 17.2 | 6 | 6 | 7 | 14 | I,2 | 6 | 13 | 25 | 38 | 31 | 13 | 26 | 39 | 37 | 38 | 38 | 36 | 37 |
| 27.0 | 4 | 6 | 5 | 14 | I,2 | 6 | 13 | 25 | 38 | 32 | 13 | 26 | 39 | 36 | 37 | 39 | 36 | 36 |
| 29.0 | 5 | 6 | 6 | 14 | I,2 | 6 | 13 | 24 | 37 | 31 | 13 | 25 | 38 | 37 | 39 | 38 | 36 | 37 |
| 41.0 | 4 | 6 | 6 | 13 | I,2 | 6 | 13 | 24 | 37 | 31 | 13 | 25 | 38 | 36 | 38 | 39 | 36 | 36 |

*DLP=dorsolateral; MDP=mid-dorsal; SLP=supralateral; LLP=lateral line; ILP=infralateral; VLP=ventrolateral; MVP=mid-ventral.

by 17.2 mm. Breast plates on the ventral surface of the abdomen and pelvic region are complete by 12.6 mm. The number of pectoral-fin base plates in *O. trispinosa* is variable ranging from 3 to 8 among specimens examined. Ossification of pectoral-fin base plates is complete by about 13.8 mm.

## Development of *Xeneretmus latifrons*

**Morphology** Larvae of *X. latifrons* are deeper bodied than *O. trispinosa*; mean body depth at the pectoral-fin origin ranges from 13.3% SL in preflexion specimens to 14.6% SL postflexion (Tables 5 and 6; Fig. 6). Head length increases from 20.3% SL in preflexion larvae to 26.6% SL in postflexion larvae, and snout length as a proportion of head length increases from 18.8% HL in preflexion larvae to 24.4% HL in postflexion larvae (Table 6). Eye diameter decreases from about 37.5% HL in preflexion larvae to 28.4% HL in postflexion larvae, and head width remains approximately 54–55% HL throughout development (Table 6).

Pectoral-fin length increases from 8.4% SL in preflexion larvae to 21.8% SL in postflexion larvae. In preflexion larvae, snout to anus distance is 51.7%

### Table 5

Morphometric measurements (in millimeters) of 45 *Xeneretmus latifrons* larvae. Specimens between dashed lines (— —) were undergoing notochord flexion.

| Standard length | Body depth | Snout to anus length | Head length | Head width | Snout length | Eye diameter | Pectoral fin length |
|---|---|---|---|---|---|---|---|
| 4.9 | 0.72 | 2.20 | 0.84 | 0.48 | 0.06 | 0.38 | 0.34 |
| 5.1 | 0.66 | 2.56 | 0.96 | 0.50 | 0.16 | 0.38 | 0.34 |
| 5.1 | 0.70 | 2.48 | 1.06 | 0.54 | 0.20 | 0.38 | 0.38 |
| 5.3 | 0.66 | 2.40 | 0.90 | 0.44 | 0.16 | 0.38 | 0.32 |
| 5.5 | 0.76 | 2.88 | 1.26 | 0.66 | 0.26 | 0.40 | 0.44 |
| 5.6 | 0.68 | 2.92 | 1.00 | 0.50 | 0.20 | 0.40 | 0.40 |
| 6.0 | 0.78 | 2.92 | 1.14 | 0.64 | 0.23 | 0.44 | 0.50 |
| 6.0 | 0.72 | 2.98 | 1.15 | 0.60 | 0.22 | 0.40 | 0.40 |
| 6.8 | 0.82 | 3.40 | 1.32 | 0.66 | 0.24 | 0.46 | 0.42 |
| 6.8 | 0.80 | 3.36 | 1.20 | 0.66 | 0.20 | 0.42 | 0.50 |
| 7.0 | 1.10 | 3.80 | 1.66 | 0.80 | 0.28 | 0.46 | 0.52 |
| 7.2 | 0.88 | 4.04 | 1.80 | 1.00 | 0.42 | 0.52 | 1.08 |
| 7.8 | 1.16 | 4.80 | 2.08 | 1.08 | 0.56 | 0.64 | 1.14 |
| 7.9 | 0.96 | 4.12 | 1.54 | 0.84 | 0.30 | 0.48 | 0.62 |
| 8.3 | 1.30 | 4.78 | 1.54 | 1.13 | 0.32 | 0.61 | 0.81 |
| 8.9 | 1.14 | 4.78 | 1.94 | 1.04 | 0.44 | 0.62 | 0.88 |
| 9.3 | 1.30 | 5.67 | 2.68 | 1.52 | 0.50 | 0.82 | 1.80 |
| 9.8 | 1.18 | 5.33 | 2.44 | 1.24 | 0.56 | 0.68 | 1.50 |
| 9.9 | 1.60 | 5.50 | 2.56 | 1.44 | 0.64 | 0.74 | 1.80 |
| 10.0 | 1.20 | 6.08 | 2.44 | 1.36 | 0.60 | 0.74 | 1.62 |
| 10.0 | 1.48 | 5.67 | 2.36 | 1.30 | 0.54 | 0.70 | 1.42 |
| 10.5 | 1.50 | 5.75 | 2.96 | 1.64 | 0.62 | 0.86 | 2.48 |
| 10.8 | 1.72 | 6.17 | 2.68 | 1.42 | 0.62 | 0.80 | 2.14 |
| 10.8 | 1.72 | 6.25 | 2.80 | 1.80 | 0.64 | 0.88 | 2.32 |
| 11.4 | 1.68 | 6.50 | 2.88 | 1.86 | 0.72 | 0.88 | 2.30 |
| 11.8 | 1.88 | 6.50 | 2.88 | 1.70 | 0.74 | 0.78 | 2.20 |
| 11.8 | 1.64 | 6.08 | 2.88 | 1.90 | 0.70 | 0.76 | 3.00 |
| 12.5 | 1.96 | 6.67 | 3.28 | 1.94 | 0.78 | 1.02 | 2.64 |
| 12.7 | 1.97 | 7.00 | 3.44 | 1.88 | 0.94 | 0.86 | 2.80 |
| 12.7 | 1.96 | 6.67 | 3.36 | 2.06 | 0.66 | 0.96 | 3.00 |
| 13.2 | 2.06 | 6.70 | 3.52 | 2.00 | 0.90 | 0.92 | 3.12 |
| 13.9 | 2.30 | 7.08 | 3.92 | 2.30 | 0.98 | 1.02 | 3.52 |
| 14.2 | 2.10 | 7.12 | 4.04 | 2.10 | 1.10 | 1.08 | 3.72 |
| 14.7 | 2.22 | 7.58 | 3.84 | 2.12 | 0.94 | 1.02 | 3.52 |
| 14.7 | 2.08 | 7.33 | 3.56 | 2.10 | 0.78 | 0.96 | 3.76 |
| 15.5 | 2.58 | 7.14 | 3.80 | 2.58 | 0.91 | 1.09 | 3.73 |
| 16.6 | 2.74 | 8.06 | 4.86 | 2.30 | 1.06 | 1.22 | 4.40 |
| 16.8 | 2.52 | 7.92 | 4.60 | 2.40 | 1.16 | 1.26 | 3.84 |
| 18.3 | 2.58 | 8.06 | 4.86 | 2.74 | 1.37 | 1.22 | 4.10 |
| 22.0 | 3.04 | 9.40 | 5.17 | 3.04 | 1.67 | 1.52 | 4.41 |
| 30.0 | 3.67 | 11.50 | 8.67 | 3.60 | 2.25 | 2.25 | 5.33 |
| 30.5 | 4.00 | 11.30 | 8.67 | 4.33 | 1.92 | 2.92 | 5.50 |
| 31.8 | 3.92 | 11.80 | 9.58 | 4.42 | 2.00 | 3.08 | 5.58 |
| 39.2 | 4.33 | 12.70 | 10.70 | 4.75 | 2.33 | 3.42 | 6.83 |
| 42.0 | 5.12 | 14.20 | 11.20 | 5.42 | 2.50 | 3.67 | 7.08 |

### Table 6

Body proportions of *Xeneretmus latifrons* larvae. Values given for each body proportion are expressed as percentage of standard length (SL) or head length (HL): mean, standard deviation, and range.

| Body proportion | Preflexion | | Flexion | | Postflexion | |
|---|---|---|---|---|---|---|
| Sample size | 15 | | 8 | | 22 | |
| Standard length | 6.3±1.1 | (4.9–8.3) | 9.9±0.6 | (8.9–10.8) | 19.0±9.4 | (10.8–42.0) |
| Body depth/SL | 13.3±1.4 | (11.9–15.7) | 14.2±1.6 | (12.1–15.9) | 14.6±1.6 | (11.0–16.6) |
| Snout to anus length/SL | 51.7±4.5 | (44.7–61.9) | 56.7±2.7 | (53.6–60.8) | 47.4±7.6 | (32.4–57.9) |
| Head length/SL | 20.3±3.0 | (17.1–26.8) | 25.3±2.3 | (21.7–28.7) | 26.6±1.8 | (23.5–30.1) |
| Head width/HL | 53.9±6.0 | (48.2–73.4) | 54.8±2.0 | (50.8–56.7) | 55.6±7.2 | (41.5–67.9) |
| Snout length/HL | 18.8±4.2 | (7.1–26.9) | 22.6±2.0 | (18.7–25.0) | 24.4±2.8 | (19.6–32.3) |
| Eye diameter/HL | 37.5±5.1 | (27.7–45.2) | 29.8±1.2 | (27.9–32.0) | 28.4±2.8 | (25.0–33.7) |
| Pectoral fin length/SL | 8.4±2.8 | (6.1–15.1) | 17.1±4.1 | (9.9–23.6) | 21.8±3.1 | (16.9–26.5) |

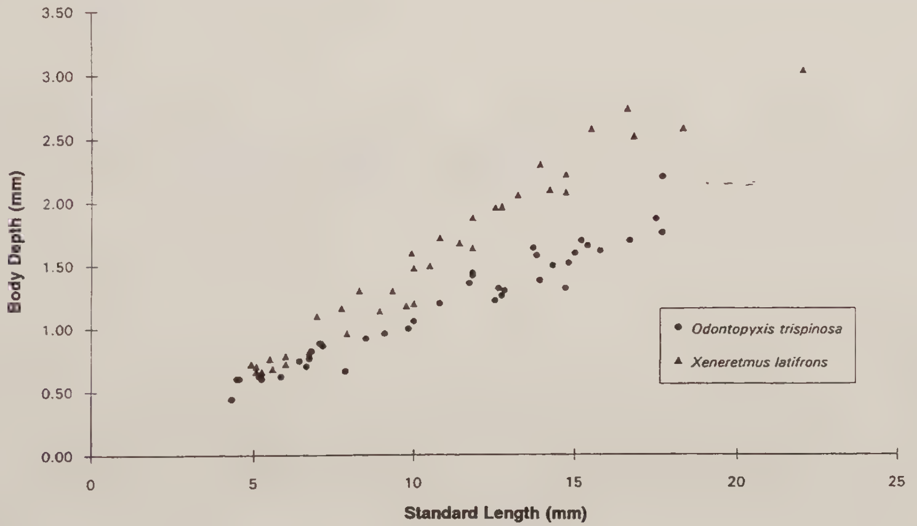

**Figure 6**

Plot of body depth vs. standard length (mm) for larval *Odontopyxis trispinosa* and *Xeneretmus latifrons*.

SL, increases to 56.7% SL during flexion, and decreases to 47.4% SL during postflexion.

**Pigmentation** Pigmentation in *X. latifrons* is consistent among specimens and is a useful distinguishing character (Fig. 7). Because pigmentation on the head and gut regions of *X. latifrons* is so similar to that described previously for *O. trispinosa*, discussion here will be limited to areas of the lateral body and fins that are diagnostically important.

**Lateral body** The lateral surface of the body above the gut in preflexion larvae is covered with melanophores, with the exception of an elongate, unpigmented area along the dorsal midline above the pectoral fin. Melanophores cover nearly the entire caudal region of the body, with the exception of the notochord tip. Melanophores extend along the dorsal and ventral margins of the unpigmented area around the notochord tip (Fig. 7A). By early flexion, melanophores completely cover the notochord tip (Fig. 7B).

Three patches of melanophores appear along the dorsal midline near the notochord tip by about 10.5 mm SL (Fig. 7C). The anterior patch forms the first band which extends from the dorsal margin of the body, posterior to the pectoral-fin base, to the anterior lateral gut area. The second band extends dorsally to connect with pigmentation seen on the first dorsal fin. The third band transverses the body between the posteriormost dorsal spine and the gut. Four or five distinct bands of pigmentation form between the anterior edges of the second dorsal and anal fins and the caudal fin. The first two bands transverse the body between the anterior and posterior margins of the second dorsal and anal fins. One or two bands are present between the posteriormost dorsal- and anal-fin rays and the hypural margin. The last band is the widest and covers the hypural region, extending into the caudal fin approximately 15–20% of its length (Fig. 7, C and D).

**Fins** Melanophores begin to appear on the ventral margin of pectoral-fin base at about 5.0 mm. The pectoral-fin base is completely covered with pigment by 6.0 mm. Pigmentation is always absent from the pectoral-fin blade, rays, and membrane (Fig. 7, A and B).

A small patch of melanophores appears in the dorsal finfold above the constriction of the gut at about 6.0mm (Fig. 7B). This pigmentation later expands and is that seen on the spinous (first) dorsal fin in late flexion and postflexion larvae (Fig. 7, C and D). Posteriorly, an additional patch of pigmentation begins about one-third of the distance between the anus and notochord tip and exhibits an irregular edge, appearing somewhat serrated, below the dorsal margin.

In preflexion larvae, a large patch of melanophores covers most of the anal finfold beginning at approximately one-fourth of the distance between the anus and notochord tip and continuing its entire length. The rela-

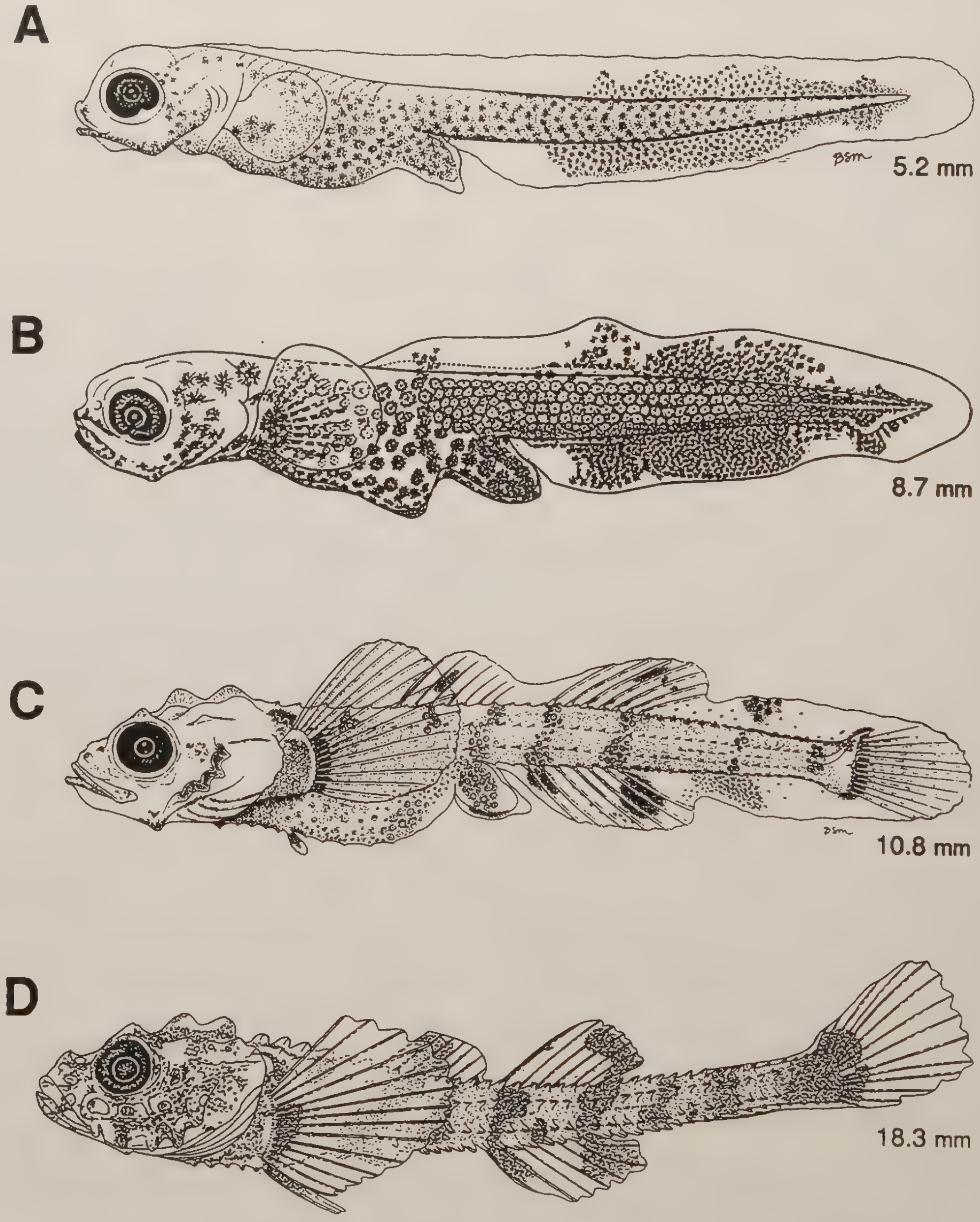

**Figure 7**

Larval stages of *Xeneretmus latifrons*. **(A)** Preflexion larva 5.2 mm SL, CalCOFI 6501BD-83.43. **(B)** Early flexion larva 8.7 mm SL, VPA, Lambert Channel 4/22/90 No. 5. **(C)** Flexion larva 10.8 mm SL, CalCOFI 5403CR-83.48. **(D)** Postflexion larva 18.3 mm SL, VPA, Lambert Channel 5/3/88 No. 4.

tively large unpigmented area anterior of this patch is an important diagnostic feature (Fig. 7, A and B).

Both the dorsal and ventral finfold melanophore patches are constricted nearly to the body margins at a point about 80%–90% of the distance between the anus and notochord tip (Fig. 7B). As notochord flexion progresses, the ventral patch of pigmentation posterior to the constriction on the anal finfold is seen as the post-hypural pigment present on the caudal fin of postflexion specimens (8.7–22.0 mm)(Fig. 7C). This caudal-fin pigmentation extends posteriorly to about 15–20% of the caudal-fin length (Fig. 7, C and D).

The remaining melanophores on the dorsal and anal finfolds migrate toward the body margins as the finfold recedes. Discrete melanophore patches remain on the anterior and posterior margins of the second dorsal and anal fins in postflexion larvae (Fig. 7D).

**Osteology** Although precursors of some bony structures such as dermal plates and fin rays are discernable as early as 8.0 mm, ossification in *X. latifrons* does not begin until approximately 13.0 mm. The sequence of ossification of bony structures in *X. latifrons* is nearly identical to that described previously for *O. trispinosa*. The most important difference to note is that ossification in *X. latifrons* begins later (13.0 mm), progresses more rapidly for lateral body plates, and is slower for most skeletal elements than *O. trispinosa*. The intent here is to highlight important differences between the two taxa.

**Cranium** All parts of the cranium, with the exception of the sphenotic, prootic, epiotic, tabular, and pterosphenoid are ossified at 13.8 mm. These remaining cranial elements ossify at about 30.5 mm.

**Mandibular region** Ossification of all mandibular structures is complete at 13.8 mm.

**Spines** Head spination is generally reduced in *X. latifrons* larvae. *Xeneretmus latifrons* larvae have no inferior infraorbital, postocular, or posttemporal plates and have only four superior infraorbital spines. The rostral spine, which is weaker than that of *O. trispinosa*, and sclerotic plates do not develop until the late postflexion stage (about 25–30 mm). The tympanic and frontal spines are more pronounced in *X. latifrons* larvae than in *O. trispinosa*.

**Palatine region** The palatine, quadrate, metapterygoid, mesopterygoid, ectopterygoid, and symplectic are ossified at 13.8 mm.

**Opercular region** The preopercle, opercle, subopercle, and interopercle are ossified by 13.8 mm.

**Hyoid region** The basihyal, hypohyal, urohyal, ceratohyal, epihyal, interhyal, glossohyal, and branchiostegal rays are ossified by 13.8 mm. The hyomandibula is ossified at 30.5 mm.

**Branchial region** The pharyngobranchial teeth, pharyngobranchials ($n$=4, fused as in *O. trispinosa*), ceratobranchials ($n$=5), and epibranchials ($n$=4) ossify at about 21.0 mm. The remainder of the branchial apparatus including the basibranchials ($n$=3) and hypobranchials ($n$=3), are ossified by 30.5 mm.

**Appendicular region** The cleithrum, postcleithrum, supracleithrum, and coracoid are ossified by 13.8 mm. Pelvic-fin spines and rays and all pectoral-fin rays are complete at 13.8 mm (Table 7). The basipterygium and posttemporal ossify by 21.0 mm. The scapula and three radials supporting the pectoral fin are ossified by 30.5 mm.

**Median fins** All dorsal-, anal-, and caudal-fin spines and soft rays are ossified by 13.8 mm (Table 7). The caudal fin has 6 superior principal, 2 superior procurrent, 6 inferior principal, and 1 inferior procurrent rays (2+6+6+1=15 total). Ossification of the hypural plate and the pterygiophores supporting the dorsal- and anal-fin rays was not complete in the largest specimen examined (39.2 mm).

**Vertebral column** Notochord flexion begins at approximately 8.5 mm and is completed by 11.0 mm. All vertebral centra and the urostyle are ossified by 13.8 mm. All except the two posteriormost neural and three haemal spines are also ossified at 13.8 mm. Ossification of all neural and haemal spines is complete by 14.5 mm (Table 7).

**Dermal plates** All dermal plates are ossified by 13.8 mm. Sequence and direction of formation and ossification is the same as previously described for *O. trispinosa*. *Xeneretmus latifrons*, however, has higher DLP+MDP, ILP, and VLP+MVP lateral body plate series counts than *O. trispinosa* (Tables 4 and 7). A maximum of five pectoral-fin plates was counted in *X. latifrons*.

## Discussion

### Summary comparison of *O. trispinosa* and *X. latifrons* larvae

Larvae of *O. trispinosa* and *X. latifrons* can be distinguished by pigmentation, morphological, and meristic characters.

Larvae of *O. trispinosa* possess a semicircular patch of melanophores that nearly covers the entire caudal finfold. This character is diagnostic and present throughout development. The caudal finfold of preflexion *X. latifrons* lacks pigmentation except for a patch located near the ventral margin of the notochord tip. This patch becomes elongate as notochord flexion progresses and becomes a band at the hypural margin. This band extends onto the caudal fin and may cover as much as 20% of its anterior surface.

Preflexion larvae of *O. trispinosa* possess a small patch of melanophores on the anal finfold immediately posterior to the origin, *X. latifrons* larvae have a large

## Table 7

Meristics of cleared and stained *Xeneretmus latifrons* larvae. Specimens between dashed lines were undergoing notochord flexion.

| Standard length (mm) | Dorsal fin | | Anal fin rays | Pectoral fin rays | Pelvic fin spines, rays | Branchiostegal rays | Neural spines | | | Haemal spines | Centra | | | Body plates* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | spines | rays | | | | | abdominal | caudal | total | | abdominal | caudal | total | DLP+MDP | SLP | LLP | ILP | VLP+MVP |
| 7.4 | | | | | | | | | | | | | | | | | | |
| 8.7 | | | | | | | | | | | | | | | | | | |
| 9.5 | | | | | | | | | | | | | | | | | | |
| 10.2 | | | | | | | | | | | | | | | | | | |
| 11.9 | | | | | | | | | | | | | | | | | | |
| 12.3 | | | | | | | | | | | | | | | | | | |
| 13.8 | 7 | 7 | 7 | 15 | I,2 | 6 | 14 | 25 | 39 | 33 | 14 | 28 | 42 | 38 | 38 | 38 | 38 | 38 |
| 14.5 | 6 | 7 | 7 | 14 | I,2 | 6 | 14 | 27 | 41 | 34 | 14 | 28 | 42 | 38 | 38 | 38 | 38 | 38 |
| 21.0 | 7 | 6 | 7 | 14 | I,2 | 6 | 15 | 26 | 41 | 35 | 15 | 27 | 42 | 41 | 41 | 41 | 40 | 41 |
| 30.5 | 7 | 7 | 7 | 15 | I,2 | 6 | 15 | 25 | 40 | 33 | 15 | 26 | 41 | 38 | 38 | 40 | 38 | 38 |
| 31.8 | 7 | 7 | 7 | 14 | I,2 | 6 | 15 | 25 | 40 | 34 | 15 | 26 | 41 | 38 | 38 | 42 | 38 | 38 |
| 39.2 | 6 | 6 | 7 | 14 | I,2 | 6 | 15 | 26 | 41 | 34 | 15 | 26 | 41 | 38 | 38 | 40 | 38 | 38 |

*DLP=dorsalateral; MDP=mid-dorsal; SLP=supralateral; LLP=lateral line; ILP=infralateral; VLP=ventrolateral; MVP=mid-ventral.

unpigmented region. Flexion and postflexion larvae of *O. trispinosa* possess a single patch of melanophores on the anal fin, *X. latifrons* have two.

Notochord flexion of *O. trispinosa* begins at approximately 7 .0mm and is completed by 11.8 mm. The largest planktonic specimens of *O. trispinosa* collected were 17.7 mm. Settlement probably occurs at approximately this size. Notochord flexion of *X. latifrons* begins at approximately 8.5 mm and is completed by 11.0 mm. The largest planktonic specimens of *X. latifrons* collected were 22.0 mm.

*Xeneretmus latifrons* larvae are deeper bodied than *O. trispinosa*. *Xeneretmus latifrons* also has a wider head than *O. trispinosa* at all stages of development. Single barbels are present at the corners of the mouth at about 15.0 mm in *O. trispinosa* and 18.0 mm in *X. latifrons*. A distinct heart-shaped occipital pit is present in *O. trispinosa* after about 15.0 mm. Postflexion larvae of each taxon are also distinguishable by adult meristic characters.

Ossification of most skeletal elements in *O. trispinosa* begins earlier and is completed at smaller sizes than in *X. latifrons*. Head spination in *X. latifrons* is generally reduced and dermal plates are absent on the head region. The caudal-fin ray complement in *X. latifrons* (2+6+6+1) is notably different than in *O. trispinosa* (3+6+6+0). Ossification of the pterygiophores supporting the dorsal and anal fins, and the hypural plate is complete by 27.0 mm in *O. trispinosa*, but was not evident in cleared-and-stained specimens of *X. latifrons* examined in this study (up to 39.2 mm). This indicates that transformation from larval to juvenile stages in *X. latifrons* occurs at much larger sizes than in *O. trispinosa*. Ossification of dermal body plates occurs in nearly identical sequence, but *X. latifrons* has more plates in the DL+MD, IL, and VL+MV series. Dermal plate formation in *X. latifrons* is complete at a slightly smaller size than in *O. trispinosa*.

The preceding descriptions eliminate the confusion in the literature concerning these larvae which resulted from previous misidentifications (page 463 of Matarese et al. (1989) and Figures A, B, and D from Marliave (1975) are larvae of *O. trispinosa* misidentified as *X. latifrons*; Figure C from Washington et al. (1984) is *X. latifrons*).

## Comparison of *O. trispinosa* and *X. latifrons* larvae with other known larval agonids

Presently, larvae of 12 of 25 agonid taxa occurring in the northeastern Pacific Ocean can be identified based on single illustrations or complete developmental descriptions. Of these 12 taxa, only *O. trispinosa* and *X. latifrons* described here are complete, illustrated at all stages of development and include discussions of ossification sequence.

By using body morphology, pigmentation, and meristic characters, larvae of *O. trispinosa* and *X. latifrons* are distinguishable from other northeastern Pacific

**Table 8**

Summary of characters useful in identifying larval and juvenile agonids from the northeastern Pacific Ocean.*

| | Characters | | | | | |
|---|---|---|---|---|---|---|
| Species | Body depth | Pectoral fin length | Pigmentation | Number of dorsal fins | Pectoral fin rays | Vertebrae |
| *Aspidophoroides monopterygius* | Slender | Elongate | Light | 1 | 9–10 | 51–53 |
| *Bothragonus swanii* | Deep | Normal | Moderate | 2 | 10–12 | 29–31 |
| *Chesnonia verrucosa* | Moderate | Elongate | Light | 2 | 14–15 | 34–38 |
| *Hypsagonus mozinoi* | Deep | Normal | Heavy | 2 | 11–12 | 34 |
| *H. quadricornis* | Deep | Normal | Heavy | 2 | 12–14 | 36 |
| *Leptagonus leptorhynchus* | Moderate | Normal | Heavy | 2 | 13–15 | 42–44 |
| *Ocella dodecaedron* | Moderate | Normal | Light | 2 | 14–16 | 38–39 |
| *Odontopyxis trispinosa* | Moderate | Normal | Moderate | 2 | 13–15 | 37–42 |
| *Percis japonicus* | Deep | Normal | Heavy | 2 | ¯12 | 40,42 |
| *Stellerina xyosterna* | Moderate | Elongate | Light | 2 | 17–19 | 34–37 |
| *Ulcina olriki* | Slender | Elongate | Moderate | 1 | 13–16 | 38–40 |
| *Xeneretmus latifrons* | Moderate | Normal | Moderate | 2 | 13–15 | 39–43 |

*Sources: Illustrations of *A. monopterygius, C. verrucosa, H. quadricornis* and *S. xyosterna* are from Washington et al. (1984); *B. swanii* is from Marliave (1975); *H. mozinoi* is from Matarese et al. (1989); *L. leptorhynchus, O. dodecaedron*, and *P. japonicus* are from Maeda and Amaoka (1988); *U. olriki* is from Dunbar (1947). Pectoral-fin ray and vertebral counts are from Matarese et al. (1989), with the exception of *H. mozinoi* and the lower count for *P. japonicus* which are from Kanayama (1991).

agonid larvae for which published illustrations are available. (Table 8). Larvae of *Hypsagonus mozinoi*, *H. quadricornis*, and *Percis japonicus* are deeper bodied, have notably shorter snout to first dorsal fin distances, are more heavily pigmented, and have lower vertebral and dermal plate counts than *O. trispinosa* and *X. latifrons* (Washington et al., 1984; Maeda and Amaoka, 1988; Matarese et al., 1989). *Bothragonus swanii* larvae have a very similar body morphology to *H. mozinoi*, *H. quadricornis*, and *P. japonicus* but have considerably less pigmentation (Marliave, 1975).

Larvae of *Chesnonia verrucosa* and *Stellerina xyosterna* have similar body morphologies to *O. trispinosa* and *X. latifrons* but have notably larger pectoral fins with bands of pigmentation on or near their posterior edges (Washington et al., 1984; Matarese et al., 1989). *Ocella dodecaedron* and *Leptagonus leptorhynchus* larvae have a similar body morphology to *X. latifrons*. However, pigmentation of *O. dodecaedron* is more sparse and that of *L. leptorhynchus* is heavier (Maeda and Amaoka, 1988).

Larvae of *Ulcina olriki* are distinguished from *O. trispinosa* and *X. latifrons* by having larger pectoral fins with pigmented edges and only a single dorsal fin (Dunbar, 1947). Larvae of *Aspidophoroides monopterygius* (= *A. bartoni*) have extremely slender bodies, a long pectoral fin with a low fin-ray count, higher vertebral and body plate counts, and a single dorsal fin (Maeda and Amaoka, 1988; Matarese et al., 1989). Studies such as this and others planned for the future are the first steps for providing diagnostic information necessary to accurately identify early life history stages of this interesting family of fishes.

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# THE EFFECT OF NATURAL VARIABILITY OF LIFE-HISTORY PARAMETERS ON ANCHOVY AND SARDINE POPULATION GROWTH

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## ABSTRACT

The northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*) populations were modeled with a stage-based matrix to examine how natural variation of life-history parameters affects per capita growth. In the model northern anchovy (*Engraulis mordax*) population, the greatest change in growth results from natural variation in the duration of, and the instantaneous mortality rate of, the early and late larval stages. In the model Pacific sardine (*Sardinops sagax*) population, the greatest change in growth results from natural variation in the duration of, and the instantaneous mortality rate of, the late larval stage. Temperature determines the duration of both egg and yolk-sac larval stages and the rate at which prerecruit sardine and anchovy mature. We believe that changes in the duration of both egg stages and yolk-sac larval stages may have greater effects on population growth than changes in any single stage.

## RESUMEN

Se modelaron las poblaciones de anchoveta nortẽna (*Engraulis mordax*) y de sardina Monterrey (*Sardinops sagax*). Usando matrices basadas en estadios de vida, se examinó como la variación natural de los parámetros de las fases vitales afecta el crecimiento per capita. En las poblaciones modelo de anchoveta, el mayor cambio en crecimiento fué resultado de la variación natural de la duración y de la tasa instantánea de mortalidad de los estadios tempranos y tardíos de las larvas. En la población modelo de sardina, el cambio mayor en crecimiento fué resultado de la variación natural de la duración y tasa instantánea de mortalidad de los estadios larvales tardíos. La temperatura determina la duración de los estadios huevo y saco vitelino, así como la tasa a la cual las sardinas y anchovetas pre-reclutas maduran. Creemos que cambios en la duración de estadios huevo y de saco-vitelino podrían tener efectos mayores en el crecimiento poblacional que cambios en cualquiera de los estadios individuales.

## INTRODUCTION

The Pacific sardine population (*Sardinops sagax*) in the northeast Pacific Ocean has greatly fluctuated during this century. Biomass peaked in 1932 at about 3,600,000 MT (Murphy 1966) and then fell to about 6,000 MT in 1975 (Barnes et al. 1992); it remained low for the rest of the decade. Recently the sardine has begun to recover off California and northern Baja California. Since the early 1980s the population has grown steadily at about 50%$\cdot$y$^{-1}$ (Smith et al. 1992) to reach a biomass of about 340,000 MT in 1991 (Barnes et al. 1992).

The northern anchovy (*Engraulis mordax*) population off California and Mexico has also undergone large changes. Stock size was low in the 1950s and 1960s, grew rapidly in the early 1970s, and reached a maximum biomass of about 1,700,000 MT in 1974 (Lo and Methot 1989). In the early 1970s, the northern anchovy's population growth rate was also about 50%$\cdot$y$^{-1}$.

Scale-deposition rates in anaerobic sediments indicate that both populations have undergone similar wide fluctuations before and since the development of modern fisheries (Soutar and Isaacs 1974; Smith and Moser 1988). Sardines appear to fluctuate more rapidly than anchovy, although Lasker and MacCall (1983) pointed out that calibrating scale-deposition rate to population size may exaggerate changes in total abundance of the species. Nevertheless the scale data indicate that large population fluctuations are common among these clupeoid stocks in the absence of fisheries, and that these fluctuations must be due to changes in the physical and biotic environment.

Global climate change will significantly affect the physical environment of marine ecosystems. Potential effects include changes in sea-surface temperature and in the intensity of upwelling (Bakun 1990). These physical changes will affect the distribution and dynamics of fish stocks. The stage-based matrix described here provides a means to test hypotheses concerning how environmental change will affect fish populations.

A number of important life-history parameters of marine fish are directly affected by changes in temperature. Temperature and food densities affect

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growth at all stages. Instantaneous mortality of eggs and larvae are also a function of temperature (Houde 1989), and the size and age of first reproduction varies with temperature (Methot 1986). Because all of these parameters are linked by temperature, it is possible that some of the effects of global climate change can be investigated by means of stage-based population models and existing knowledge.

Previous attempts to model anchovy or sardine populations using stage-based models have been hampered by (1) a lack of theoretical framework (Smith 1985) or (2) an incomplete understanding of the range of variation for important life-history parameters (Smith 1985; Smith et al. 1992). Our objective in this paper is to model anchovy and sardine populations by using a stage-based matrix (Lefkovitch 1965) as a theoretical framework and to examine how natural variation of stage-specific vital rates affects population growth rates.

Vital rates for each stage of the model were obtained from the literature. For some stages the vital rate is unknown; in such cases we obtained a vital rate from literature on other populations of sardines and anchovy, or estimated by the methods described below. We have thus compiled the most comprehensive estimates of life-history parameters to date. We also examined the effect of fishing mortality on the two populations.

## METHODS

The matrix (**A**) describes the transition of a population from time $t$ to time $t+1$ in terms of vital rates of each life stage:

$$\mathbf{A}n_t = n_{t+1} \qquad (1)$$

where $n_t$ is a vector describing the population at each stage at time $t$, and **A** is the transition matrix:

$$\mathbf{A} = \begin{array}{cccccc} P_1 & m_2 & . & . & . & m_q \\ G_1 & P_2 & 0 & . & 0 & 0 \\ 0 & G_2 & P_3 & 0 & . & 0 \\ . & . & . & . & . & . \\ 0 & 0 & 0 & . & G_{q-1} & P_q \end{array} \qquad (2)$$

where $P_i$ is the probability of surviving and staying in stage $i$, $G_i$ is the probability of surviving and growing into the next stage, and $m_i$ is the maternity per fish per unit time (d); $i = 1, . . q$.

Both $P_i$ and $G_i$ are functions of the survival probability ($p_i$) and the growth probability ($\gamma_i$) (Caswell 1989):

$$p_i = e^{-z_i} \qquad (3)$$

and $$P_i = p_i(1 - \gamma_i) \qquad (4)$$

and $$G_i = p_i\gamma_i \qquad (5)$$

where $$\gamma_i = [(1 - p_i)p_i^{d_i-1}]/[1 - p_i^{d_i}] \qquad (6)$$

where $z_i$ is the daily instantaneous mortality rate (IMR) and $d_i$ is the duration ($d$) within the ith stage. The derivation of $P_i$, $G_i$, and $\gamma_i$ follow Crouse et al. (1987) and Caswell (1989).

The maternity parameter $m_i$ is computed as:

$$m_i = (\sum_j[f_j w_{ij}])/\sum_j[w_{ij}] \qquad (7)$$

where $f_j$ (the age-specific fecundity rate) is the number of eggs per fish of age $j$ per unit time, and $w_{ij}$ is the proportion of fish that are of age $j$:

$$w_{ij} = \exp(-z_i t_{1j}) - \exp(-z_i t_{2j}) \qquad (8)$$

where $t_{1j}$ is the beginning and $t_{2j}$ is the ending age for the fish of age group $j$. Briefly, total annual production of eggs was estimated for each size class and apportioned on an average daily basis.

Anchovy spawn each day from sunset to midnight, with the peak at 2200 (Lo 1983). Sardine spawn between 2000 and 0400, with the peak near midnight (Smith 1973). In the model, the fecundity estimates of sardine were assumed to be knife-edged at 0000 h, and the fecundity estimates of anchovy were corrected for mortality from spawning (2200) to census at the end of day one (2400) by: $F_i = Q_i m_i$, where $Q_i$ is the probability of surviving from spawning to the first census and $Q_i = e^{-zt}$, where $z$ is the daily instantaneous mortality rate and $t$ is the time from peak spawning to the time of census.

The dominant eigenvalue $\lambda$ of the matrix represents the population growth rate. If $\lambda = 1.0$, the population is stationary, and if $\lambda = 1.5$, the population is growing at 50%·d$^{-1}$. The results are given in annual growth of the population, which is equal to $\lambda^{365}$, since the duration of stages was measured in days. We estimated $\lambda$ from the dominant eigenvalue of the matrix **A** using MathCAD.

We measured the importance of natural variability in mortality, duration, and fecundity parameters at each stage by calculating $\lambda$ for a series of values for each parameter. Initial conditions were a stationary population, and we examined changes of $\lambda$ with known deviations of each stage-specific vital rate.

### *Anchovy Vital Rates*

The northern anchovy is a multiple spawner (Hunter and Goldberg 1980). Annual fecundity is the number of eggs released per spawning (batch fecundity) times the number of spawnings in a season. The variation in batch fecundity and the variation of spawning rate with age are well known (Hunter and Goldberg 1980; Hunter and Macewicz 1980; Parrish et al. 1986; Alheit, in press), but little is known of the interannual variation in number of spawnings per year. The spawning rate for northern anchovy varies interannually from once every 6.25 days to once every 10.6 days (Bindman 1985). At that rate the average female would spawn 5 to 10 times during the March–April spawning season. Some spawning occurs all year long, and Parrish et al. (1986) found evidence that the number of spawnings per year increases with age. The fecundity used in the model was a daily rate that apportioned spawning equally over the year (table 1). In reality, spawning is seasonal, but modeling the seasonality of spawning is beyond the scope of this paper. The daily fecundity was divided by two to estimate the number of female eggs.

The anchovy population was modeled on the basis of nine stages, as defined by Smith (1985). We derived minimum, maximum, and best estimates of daily instantaneous mortality rates and duration of each stage from literature values (table 2). The durations of the egg and yolk-sac stages are derived from incubation experiments at different temperatures (Lo 1983). Mean duration was based on the development rate at 16°C, which is about the average temperature for anchovy eggs. Mortality rates of egg, yolk-sac, and larval stages were estimated from field studies (Stauffer and Picquelle 1981; Bindman 1985). Durations of the larval and juvenile stages are from field studies of growth rates derived from daily increments in the otoliths (Methot and Kramer 1979; Butler 1987, 1989).

TABLE 1

Fecundity Schedule of Northern Anchovy

| Year | Wt (g) | Spawns per year | Batch (eggs) | $M(x)$ | $L(x)$ $z = .76$ | $LxMx$ | Daily |
|---|---|---|---|---|---|---|---|
| 0 | 0.0 | 0.0 | | | | | |
| 1 | 8.7 | 5.3 | 4237.8 | 22460.3 | 1000 | 11230170 | 30747 |
| 2 | 14.6 | 11.9 | 7860.4 | 93538.8 | 468 | 21888070 | 59926 |
| 3 | 18.3 | 19.2 | 10132.2 | 194538.2 | 216 | 21010130 | 57523 |
| 4 | 21.2 | 23.5 | 11912.8 | 279950.8 | 102 | 14277491 | 39090 |
| 5 | 24.5 | 23.5 | 13939.0 | 327566.5 | 48 | 7861596 | 21524 |
| 6 | 24.5 | 23.5 | 13939.0 | 327566.5 | 22 | 3603232 | 9865 |
| 7 | 24.5 | 23.5 | 13939.0 | 327566.5 | 10 | 1637833 | 4484 |

| | Female eggs per female per day mean | 90% maturity at year one* |
|---|---|---|
| Juveniles | 11.7 | 10.5 |
| Small adults | 199.2 | 199.2 |
| Large adults | 448.4 | 448.4 |

*Assuming that 90% of females mature at age 1 and that the batch fecundity is given by the formula: Batch = −1104 + 614*wt (Hunter et al. 1985).

Mortality rates of the late larval and early juvenile stages are unknown. We estimated these rates from the relationship of mortality rate to body size (Peterson and Wroblewski 1984) and adjusted them to achieve a stationary population. The relationship between dry weight and mortality rate is given by Peterson and Wroblewski (1984): $M_{(w)} = (1.92 \cdot y^{-1})w^{-0.25}$, and the relation between length and dry weight for northern anchovy is dry weight = 0.000488*SL^3.73, where SL is measured in cm (Butler 1987). For a 72.5-mm juvenile $M = 2.04$, and the daily rate is $z = 2.83/365.25 = 0.00557$. This value was adjusted to a "best" value of 0.0044 to obtain a lambda of 1.0. We chose the late juvenile stage for this adjustment because at present little is known about natural mortality in this stage.

TABLE 2

Stage-Specific Life-History Parameters of Northern Anchovy

| Stage | Size (mm) | | Daily natural mortality | | | Duration (days) | | | Daily fecundity/female | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Min. | Max. | Min. | Best | Max. | Min. | Best | Max. | Min. | Best | Max. |
| Egg | | | 0.12[a] | 0.231[a] | 0.45[b] | 1.4[c] | 2.9[c] | 3.9[c] | 0 | 0 | 0 |
| Yolk-sac larvae | hatch | 4 | 0.19[d] | 0.366[d] | 0.59[d] | 1.4[c] | 3.6[c] | 3.9[c] | 0 | 0 | 0 |
| Early larvae | 4 | 10 | 0.187[d] | 0.286[d] | 0.345[d] | 8[e] | 12[e] | 23[e] | 0 | 0 | 0 |
| Late larvae | 10 | 35 | 0.0470[f] | 0.0719[f] | 0.087[f] | 35[g] | 45[g] | 71[g] | 0 | 0 | 0 |
| Early juvenile | 35 | 60 | 0.0009[f] | 0.0141[*] | 0.017[f] | 45[g] | 62[g] | 100[g] | 0 | 0 | 0 |
| Late juvenile | 60 | 85 | 0.0029[f] | 0.0044[f] | 0.0053[f] | 60[g] | 80[g] | 138[g] | 0 | 0 | 0 |
| Prerecruit | 85 | 110 | 0.0020[f] | 0.0031[f] | 0.0037[f] | 200[h] | 287[h] | 632[h] | 0 | 10.[i] | 19.4 |
| Early adult | 110 | 135 | 0.0011[j] | 0.0021[j] | 0.0036[j] | 750[h] | 1000[h] | 1250[h] | 143.8 | 199.2[i] | 230.7 |
| Late adult | 135 | 160 | 0.0011[j] | 0.0021[j] | 0.0036[j] | 1000[h] | 1250[h] | 1500[h] | 284.2 | 448.2[i] | 529.0 |

[a] Bindman 1985
[b] Stauffer and Picquelle 1981
[c] Lo 1986
[d] Peterman et al. 1988
[e] Methot and Kramer 1979
[f] Peterson and Wroblewski 1984
[g] Butler 1987, Waldron et al. 1989
[h] Fiedler et al. 1986
[i] Hunter et al. 1985
[j] Methot 1989
*Used to tune model to lambda = 1.0

Adult natural mortality rates are assumed to be constant with age and were derived from the stock synthesis model (Methot 1989). We also examined the effect of an annual fishing mortality rate of 0.6 on all adult stages. We derived adult growth rates from fisheries data (Fiedler et al. 1986).

### *Sardine Vital Rates*

Pacific sardine is also a multiple spawner. Batch fecundity estimates were based on MacGregor (1957) and Clark (1934). Little is known about the number of spawnings per year. Off Chile, the Pacific sardine (*S. sagax musica*) spawns every 7 days (Oliva et al. 1989), a rate similar to that of the northern anchovy. The South African pilchard, *Sardinops ocellatus*, spawns every 2–5 days, and older fish may spawn up to 80 times per year (Le Clus 1989). Fecundities in the life table (table 3) were estimated from batch fecundity times a total of 40 spawnings per year for the oldest age classes (the maximum rate is 80 spawnings per year, and the minimum is 24; table 4). We divided the daily fecundity by two to account for the number of female eggs.

We modeled the sardine population with thirteen stages as defined by Smith et al. (1992). The minimum, maximum, and mean daily instantaneous mortality rates and duration of each stage are derived from the literature (table 4). The durations of the egg and yolk-sac stages are derived from incubation experiments at different temperatures (Lasker 1964). Mean duration was derived from the development rate at 16°C, which is about the average temperature for sardine eggs (15.6°C; Butler 1987). We estimated mortality rates of yolk-sac and larval stages from the field (Butler 1991). The best estimates of egg mortality rates are from unpublished data (N. C. H. Lo). Durations of the larval and juvenile stages are from field studies of growth rates calculated from daily increments in the otoliths (Butler and Rojas de Mendiola 1985; Castillo et al. 1985; Butler 1987). The mortality rates of the late larvae through stage III juveniles are unknown. We estimated these rates from the general relation-

TABLE 3

**Fecundity Schedule of Pacific Sardine**

| Age | Wt (g) | Spawns | Batch | *M(x)* | Daily | *L(x)* | Survivors to day 1 |
|---|---|---|---|---|---|---|---|
| 1 | 52.7 | 0 | 13860 | 0 | 0 | 1000 | 0 |
| 2 | 93 | 6 | 24459 | 146754 | 402 | 670 | 201 |
| 3 | 123 | 12 | 32349 | 388188 | 1063 | 449 | 238774 |
| 4 | 152 | 15 | 39976 | 599640 | 1642 | 301 | 247239 |
| 5 | 170 | 19 | 44710 | 849490 | 2326 | 202 | 234783 |
| 6 | 193 | 23 | 50759 | 1167457 | 3196 | 135 | 216288 |
| 7 | 202 | 28 | 53126 | 1487528 | 4073 | 91 | 184730 |
| 8 | 205 | 30 | 53915 | 1617450 | 4428 | 61 | 134644 |
| 9 | 205 | 35 | 53915 | 1887025 | 5166 | 41 | 105297 |
| 10 | 205 | 40 | 53915 | 2156600 | 5904 | 27 | 80666 |
| 11 | 205 | 40 | 53915 | 2156600 | 5904 | 18 | 54072 |
| 12 | 205 | 40 | 53915 | 2156600 | 5904 | 12 | 36245 |
| 13 | 205 | 40 | 53915 | 2156600 | 5904 | 8 | 24296 |

|  | Female eggs per female per day | Survivors to first census |
|---|---|---|
| Prerecruit | 134 | 80.5 |
| Juveniles | 647.6 | 388.9 |
| Small adults | 1576.3 | 946.6 |
| Large adults | 2811.5 | 1688.3 |

Batch fecundity = 263 eggs per gram (MacGregor 1957).

TABLE 4

**Stage-Specific Life-History Parameters of the Pacific Sardine**

|  | Size (mm) |  | Daily natural mortality |  |  | Duration (days) |  |  | Daily fecundity/female |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Stage | Min. | Max. | Min. | Best | Max. | Min. | Best | Max. | Min. | Best | Max. |
| Egg |  |  | 0.31[a] | 0.72 | 2.12[b] | 1.4[c] | 2.5[c] | 3.9[c] | 0 | 0 | 0 |
| Yolk-sac larvae | hatch | 4 | 0.394[d] | 0.6698[d] | 0.971[d] | 1.4[c] | 3.1[c] | 3.9[c] | 0 | 0 | 0 |
| Early larvae | 4 | 10 | 0.1423[d] | 0.2417[d] | 0.3502[d] | 5[e] | 11[e] | 21[f] | 0 | 0 | 0 |
| Late larvae | 10 | 35 | 0.057[d] | 0.0964[d] | 0.139[d] | 20[g] | 35[g] | 50[g] | 0 | 0 | 0 |
| Early juvenile | 35 | 60 | 0.029[d] | 0.056[d] | 0.081[d] | 17[g] | 25[g] | 40[g] | 0 | 0 | 0 |
| Juvenile I | 60 | 85 | 0.0116[h] | 0.0197[h,*] | 0.0285[h] | 30[g] | 50[g] | 80[g] | 0 | 0 | 0 |
| Juvenile II | 85 | 110 | 0.0023[h] | 0.0040[h] | 0.0058[h] | 80[g] | 110[g] | 146[g] | 0 | 0 | 0 |
| Juvenile III | 110 | 135 | 0.0016[h] | 0.0028[h] | 0.0040[h] | 105 | 146[g,i] | 185 | 0 | 0 | 0 |
| Juvenile IV | 135 | 160 | 0.0012[j] | 0.0022[j] | 0.0032[j] | 110 | 170[i] | 220 | 0 | 0 | 0 |
| Prerecruit | 160 | 185 | 0.0006[l] | 0.0011[l] | 0.0015[l] | 110 | 175[i] | 220 | 0 | 80[k] | 161[k] |
| Early adult | 185 | 210 | 0.0006[l] | 0.0011[l] | 0.0015[l] | 190[m] | 381[m] | 570[m] | 286[k] | 389[k] | 489[k] |
| Adult | 210 | 235 | 0.0006[l] | 0.0011[l] | 0.0022[l] | 400[m] | 663[m] | 920[m] | 730[k] | 946[k] | 1114[k] |
| Late adult | 235 | 260 | 0.0006[l] | 0.0011[l] | 0.0022[l] | 1908[m] | 2773[m] | 3473[m] | 1064[k] | 1688[k] | 3123[k] |

[a] Smith 1973
[b] Smith et al. 1989
[c] Lasker 1964
[d] Butler 1991
[e] Butler and Rojas de Mendiola 1985
[f] Castillo et al. 1985
[g] Butler 1987
[h] Peterson and Wroblewski 1984
[i] Kimura and Sakagawa 1972
[j] By analogy to northern anchovy
[k] MacGregor 1957, Clark 1934, Le Clus 1989
[l] Murphy 1966, MacCall 1979
[m] Walford and Mosher 1943, Phillips 1948
*Used to tune model to lambda = 1.0

ship of mortality rate to body size (Peterson and Wroblewski 1984). The relationship between dry weight and length is given by: dry weight = 0.0122*SL^3.35, where standard length is measured in cm (Butler 1987). The predicted mortality rate was 0.0053 for stage I juveniles, and we adjusted this value to 0.0197 to achieve a theoretically stationary population. The mortality rates of stage IV juveniles and prerecruits are assumed to be the same as the mortality rates for northern anchovy of the same body size. Adult growth rates were derived from otolith readings (Phillips 1948); adult mortality rates were derived from the cohort analysis (Murphy 1966; MacCall 1979). Natural mortality was set at 0.4%$\cdot$y$^{-1}$. We also examined the effect of annual fishing mortality rates of 0.25 and 0.6.

## RESULTS

### *Anchovy*

Natural variations in individual stage-specific mortality or duration (table 5) result in changes of population growth from equilibrium to an annual increase or decrease of about threefold. The most influential stage appears to be the early larval. Natural variation in instantaneous mortality rates or duration of this stage lead to the largest changes in the population growth rate. The fastest growth rate of the early larvae results in a 278% increase in the population, whereas the slowest growth rate results in a 74% decrease (table 5). The least sensitive is the late adult stage: at that point, variations in growth and mortality have minimal effect on population growth. The sensitivity of the model to natural variations in fecundity may be an underestimate. The values in the literature are largely taken from biomass estimate studies, and none of these studies has encompassed a major environmental perturbation. There is some evidence that reproduction is drastically reduced during major El Niño events. Under such conditions the population declines rapidly.

TABLE 5

**Eigenvalue ($\lambda^{365}$) of Lefkovitch Matrix after Change in the Stage-Specific Life-History Parameters of Northern Anchovy**

| Stage | Natural mortality | | Duration | | Fecundity | |
|---|---|---|---|---|---|---|
| | Min. | Max. | Min. | Max. | Min. | Max. |
| Egg | 1.27 | 0.66 | 1.30 | 0.85 | | |
| Yolk-sac larvae | 1.65 | 0.60 | 1.93 | 0.93 | | |
| Early larvae | 2.78 | 0.64 | 2.67 | 0.26 | | |
| Late larvae | 2.57 | 0.65 | 1.78 | 0.37 | | |
| Early juvenile | 1.90 | 0.88 | 1.20 | 0.71 | | |
| Late juvenile | 1.09 | 0.95 | 1.07 | 0.85 | | |
| Prerecruit | 1.35 | 0.84 | 0.98 | 0.79 | 0.95 | 1.02 |
| Early adult | 1.06 | 0.95 | 1.06 | 0.97 | 0.86 | 1.12 |
| Late adult | 1.00 | 1.00 | 1.00 | 1.00 | 0.97 | 1.16 |

TABLE 6

**Eigenvalue ($\lambda^{365}$) of Lefkovitch Matrix after Change in the Stage-Specific Life-History Parameters of Pacific Sardine**

| Stage | Natural mortality | | Duration | | Fecundity | |
|---|---|---|---|---|---|---|
| | Min. | Max. | Min. | Max. | Min. | Max. |
| Egg | 1.29 | 0.68 | 1.21 | 0.84 | | |
| Yolk-sac larvae | 1.23 | 0.85 | 1.34 | 0.90 | | |
| Early larvae | 1.31 | 0.82 | 1.47 | 0.72 | | |
| Late larvae | 1.43 | 0.79 | 1.47 | 0.79 | | |
| Early juvenile | 1.17 | 0.89 | 1.11 | 0.89 | | |
| Juvenile I | 1.15 | 0.95 | 1.09 | 0.89 | | |
| Juvenile II | 1.04 | 0.96 | 1.03 | 0.97 | | |
| Juvenile III | 1.04 | 0.96 | 1.03 | 0.98 | | |
| Juvenile IV | 1.04 | 0.97 | 1.03 | 0.98 | | |
| Prerecruit | 1.02 | 0.98 | 1.01 | 0.99 | 0.98 | 1.00 |
| Early adult | 1.04 | 0.97 | 1.03 | 0.98 | 1.00 | 1.00 |
| Adult | 1.05 | 0.91 | 1.01 | 0.99 | 1.00 | 1.01 |
| Late adult | 1.05 | 0.86 | 0.99 | 1.00 | 1.00 | 1.11 |

We tested the effect of fishing on the anchovy population by using values of natural mortality of 0.76 and fishing mortality of 0.6 for both adult stages. Under these conditions the anchovy population declined at a rate of 5%$\cdot$y$^{-1}$.

### *Sardine*

The population growth rate of the Pacific sardine appears to be most sensitive to changes in egg and larval stages (table 6). Reported values for egg mortality vary widely in the literature (Smith 1973; Smith et al. 1989). Extremely high values of egg mortality—88% in the first day—were reported for the Pacific sardine off Peru (Smith et al. 1989). At this rate the model indicates that the population declines at the rate of 32% per year. The fastest growth of the early and late larval stages results in population growth rates of 43%$\cdot$y$^{-1}$, whereas the slowest growth rate of the early larval stage results in a population decrease of 28%$\cdot$y$^{-1}$ (table 6). The population is least sensitive to changes in the vital rates of the older stages, prerecruit through late adult.

Fishing affects the mortality rate of all adult sardine stages. If fishing mortality is 0.25, then the population declines at a rate of 18%$\cdot$y$^{-1}$. During the decline of the sardine fishery, fishing mortality was as high as 0.8 (Murphy 1966). At this level, the population declines at 50%$\cdot$y$^{-1}$. High fishing mortality reduces the abundance of the oldest age classes, which have the highest reproductive potential because of their larger size and greater number of spawnings.

## DISCUSSION

For the northern anchovy, natural variation in the duration of, and the instantaneous mortality rate of the early and late larval stage has the greatest effect on population growth (table 5). These results are similar to those of Smith (1985), who used a stage-based model to examine the role of vital rates in the dynamics of anchovy recruitment. Smith concluded that changes in the late larval stage have the greatest potential to affect survival and recruitment. Our results indicate that the anchovy population is also sensitive to changes in the early larval stage (table 5). The difference between our model and Smith's (1985) is largely due to the low mortality rate (0.16) that Smith used for this stage. The higher mean mortality rate (0.29) in our model leads to greater sensitivity, since faster or slower growth rates have a greater cumulative effect. High abundance of the early larval stage is a prerequisite to strong recruitment, but high larval abundance does not necessarily indicate strong year classes (Peterman et al. 1988).

In this model, we have also tried to examine the role of changes in fecundity. The variation in batch fecundity and spawning rate with age are well known, but little is known of interannual variability in the number of spawns per year. Estimated spawning rates for northern anchovy have varied from once every 6.25 days to once every 11 days. However, the Japanese anchovy, *Engraulis japonica*, spawns once every 1.4 days, and the Cape anchovy, *Engraulis capensis*, spawns as seldom as once every 16 days. Clearly, the number of spawns can vary significantly.

The sensitivity of the anchovy population matrix to changes in the vital rates of both early and late larvae is due to the dynamics of these stages. Natural mortality is high (Peterman et al. 1988), and the duration is long relative to egg stages. Changes in either value produce large effects. The observed natural variation in mortality rate of the early stage is quite large. Smith (1985) also identified the late larval stage of anchovy as important to recruitment variation. Variation in the duration of this stage is largely due to changes in temperature rather than difference in food densities (Methot and Kramer 1979; Owen et al. 1989).

Most life-table parameters do not change independently. The development rate of northern anchovy eggs and yolk-sac larvae is temperature-dependent (Zweifel and Lasker 1976, Lo 1986), as are larval growth rates (Methot and Kramer 1979). At about 22°C the egg, yolk-sac, and early larval stages would be brief. If all these stages are at their lower limits, the model population more than doubles each year. The population model can be stabilized if reproduction is restricted to the prerecruit stage (85–110 mm), with fecundity reduced to only 7 eggs per female per day. In other words, these life-history parameters are then similar to those of a small tropical anchovy, *Encrasicolina purpurea* (Clarke 1989; Somerton, in press).

From 1922 to 1942, temperatures at Scripps Pier averaged 17.1°C; from 1943 to 1974, temperatures averaged 16.6°C, excluding El Niño years 1957–59. The duration of both incubation and the yolk-sac stage are a function of temperature (Lasker 1964; Zweifel and Lasker 1976). Given these relationships, the Lefkovitch model, adjusted to stability at colder temperatures (11°C), predicts that the northern anchovy population would grow at an annual rate of 7% during warmer years (22°C), and that the sardine population would grow at $4\%\cdot y^{-1}$. Thus, temperature effects on the early stages alone cannot explain the difference in abundance of the two species from 1922 to 1942 and from 1943 to 1973. Temperature's effect on spawning rates in both species is unknown, as are its effects on the age of maturation and on the growth rate of juveniles.

The sardine population appears to be less sensitive to changes in vital rates than the anchovy population by an order of magnitude. Changing the duration of the early larval stage changes growth rates by $+40\%$ or $-27\%\cdot y^{-1}$. The addition of fishing mortality results in a $44\%\cdot y^{-1}$ decline in the population. Clark and Marr (1955) debated whether the environment or fishing caused the decline of the sardine population. Our results indicate that either the environment or fishing can produce these changes.

Some discussion of the assumptions of this model is warranted. The stage-specific model assumes that the population reaches a stable age distribution. In reality, stage-specific life-history parameters vary from year to year, and the population probably never achieves a stable age distribution. The fecundity estimates are averaged over all seasons and assumed to be constant on a daily basis. In reality, fecundity has a seasonal component, and most fecundity estimates are made during the peak season. It is also important to note that these fecundity estimates have been made during the course of biomass estimates and that few, if any, long-term studies exist. There is some indication that fecundity may be near zero during extreme environmental conditions (Csirke 1980; Ware and Tsukayama 1981).

The model also does not treat density-dependent effects. Growth rates predicted by the model are not sustained indefinitely in nature. Density-dependent effects on the population could be modeled by changing fecundity, mortality, or duration with population size. The model's sensitivity to changes in the larval stages suggests that cannibalism may be an important density-dependent feedback mechanism. Density-dependent influences are usually weak compared to density-independent factors, but MacCall (1981), Alheit (1987), Valdés et al. (1987), and Valdés Szeinfeld (1991) have indicated that cannibalism is an important density-dependent effect in clupeoid fishes. Cannibalism on eggs may, in fact, be largely density-independent (Smith et al. 1989), whereas cannibalism on larvae from different schools, because of the population's sensitivity to larval mortality rates, may be density-dependent.

## CONCLUSIONS

Natural variation in stage-specific vital rates can account for the large changes in population size observed in nature. The Lefkovitch model predicts changes in population growth that are as great as those indicated by the time series of these populations. Both populations are more sensitive to variation in the parameters of larval stages than to adult parameters. However, more research is needed on interannual variation of adult reproductive parameters, since these variations may have greater impact than indicated in the present model.

The sensitivity of the models to larval duration and mortality rate does not, however, indicate that these stages can be used to predict recruitment. Variance of postmetamorphic stages is sufficient to mask the relation between larval abundance and subsequent recruitment. These results are in accordance with those of Bradford (1992).

Many of these vital rates covary. Durations of both the egg and yolk-sac stages are temperature-dependent, and the maturation and spawning rates also vary with temperature. Changes in the ambient temperature could significantly change the life history of these species.

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# A Review of the Commercial Fisheries for Sharks on the West Coast of the United States

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## Abstract

Six species presently dominate commercial fisheries for sharks off the western United States. The oldest of these fisheries (for soupfin shark, *Galeorhinus zyopterus* [=*galeus*]) was decimated in 1944 but has persisted for the past two decades on a small scale, averaging between 150,000 and 250,000 pounds (~68-114 MT) annually. The largest (for spiny dogfish, *Squalus acanthias*) has consistently produced landings in excess of 5 million lbs (~2273 MT) annually. The blue shark (*Prionace glauca*) fishery, in operation experimentally between 1979 and 1980, now is part of a long-line operation with markets still being explored. A drift gill net and experimental long-line fishery targets on common thresher shark (*Alopias vulpinus*) and shortfin mako shark (*Isurus oxyrinchus*). Declines in catches and size composition of the common thresher fishery have required serious management actions such as time/area closures, permit limitations, and low total allowable landings. The shortfin mako shark fishery has not seriously declined, but only takes one, two and sometimes three year old sharks. Landings of Pacific angel sharks (*Squatina californica*) in a localized bottom gill net fishery peaked in 1985 and 1986 at 1.2 million lbs (~546 MT) annually, but drastically declined due to decreased availability and alternative sources of low-cost, imported shark meat. The leopard shark (*Triakis semifasciata*), another common inshore species, is fished both recreationally and commercially, with its landings fluctuating between 18,000 and 100,000 lbs (~8-46 MT) per year, but no significant decline. Thus, total west coast shark landings increased steadily through 1985, but have since declined. Declines have occurred mainly because slow growth, low fecundity and late age at maturity make elasmobranchs vulnerable to overfishing.

## Introduction

Recent fisheries for elasmobranchs along the west coast of the United States began in the late 1970s and have continued to the present (Cailliet and Bedford 1983, Holts 1988). There were early warnings that these fisheries would most likely suffer from over- exploitation during early development (Holden 1974, 1977, Cailliet and Bedford 1983). The fisheries continued to expand until problems were very evident.

Elasmobranchs have low reproductive rates due to their low fecundity, slow growth rates, and late age of maturity (Holden 1974, 1977). These qualities, along with a natural inquisitiveness and lack of fear, make them vulnerable to overfishing (Anderson 1990, Compagno 1990). After the decline of the soupfin shark (*Galeorhinus zyopterus* [ = *G. galeus*, Eschmeyer et al. 1983]) fishery for vitamin A-rich liver oil in the 1940s, sharks were viewed as a resource of little value. In the late 1970s, popular interest in shark meat created new market demands. Domestic landings and imports of numerous shark species increased several fold during the last decade and have since declined (Holts 1988). Although the reasons for these variations are many, the most identifiable are market fluctuations and susceptibility of these stocks to over-exploitation.

It is now obvious that the management options taken were insufficient to prevent the predicted declines (Bedford 1987, Richards 1987, Holts 1988). Because of this, there is an increasing need for careful monitoring of exploited shark populations on the west coast to prevent stock depletion in these fisheries similar to actions now proposed for the east and gulf coasts of the United States (Hoff and Musick 1990). Two west coast shark species (common thresher, *Alopias vulpinus* and Pacific angel, *Squatina californica*) show signs of depletion and others are being harvested at near-record levels.

The purpose of this paper is to: 1) update the status of these fisheries, based upon catch data collected by the fisheries agencies for the three west-coast states and the United States National Marine Fisheries Service (National Oceanic and Atmospheric Administration); 2) describe current management strategies and regulations; and 3) propose ideas that can be used to effectively regulate elasmobranch fisheries.

### General Trends in West Coast Shark Fisheries

Shark landings along the west coast of the United States increased steadily through 1985, but have since declined (Table 1, Figure 1).

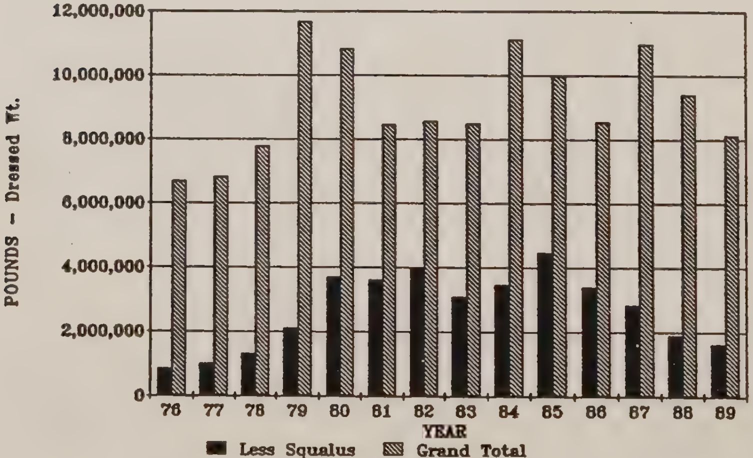

Fig. 1. Trends in annual west coast commercial shark landings ( in pounds, dressed weight) from 1976 through 1989.

Early landings were almost 7 million pounds (~3,180 Metric Tons) in 1976 and 1977, followed by later peaks at approximately 11 million lbs (~5,000 MT) in four different years (1979, 1980, 1984, and 1987).

Currently, landings are about 8 million pounds (~3,636 MT). For the entire coast, these trends closely followed those of the spiny dogfish (*Squalus acanthias*), which has consistently represented the largest portion of the shark catch. The next most

Table 1. West coast commercial shark landings (in pounds) from 1976 through 1989.

| Species | 1989 | 1988 | 1987 | 1986 | 1985 | 1984 | 1983 | 1982 | 1981 | 1980 | 1979 | 1978 | 1977 | 1976 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pacific Angel | 268,252 | 491,348 | 940,187 | 1,241,130 | 1,237,810 | 633,250 | 351,344 | 317,953 | 260,031 | 110,022 | 123,652 | 82,383 | 366 | 690 |
| Thresher, Bigeye | 22,093 | 12,033 | 25,303 | 46,184 | 119,632 | 74,769 | 106,507 | 36,269 | 10,542 | 10,842 | | | | |
| Blue | 13,621 | 7,270 | 3,907 | 2,850 | 2,356 | 3,940 | 13,983 | 57,838 | 202,898 | 192,130 | 83,966 | 35,904 | 98,365 | 9,928 |
| Mako, Shortfin | 388,322 | 489,217 | 612,020 | 456,063 | 215,126 | 244,021 | 322,953 | 527,677 | 275,830 | 155,336 | 35,334 | 27,436 | 19,911 | 2,293 |
| Smoothhound, Brown | 10,967 | 15,522 | 12,916 | 13,506 | 33,312 | 8,091 | 14,101 | 5,263 | 23,641 | 5,783 | 2,440 | 7,365 | 264 | 20 |
| Thresher, Common | 655,078 | 639,773 | 770,092 | 1,215,165 | 1,528,766 | 1,662,587 | 1,757,353 | 2,386,585 | 1,937,618 | 1,806,002 | 735,602 | 302,073 | 129,522 | 46,887 |
| Cow | 131 | 156 | 358 | 439 | 427 | 1,333 | 1,258 | 1,328 | 771 | 438 | 290 | 249 | | 35 |
| Dusky | | | | | | | 120 | | 196 | | | 103 | 202 | 50 |
| Smoothhound, Grey | 412 | 20 | | 506 | 1,874 | 6,846 | 1,055 | 2,520 | | 761 | 12,046 | 33,745 | | |
| Horn | 32 | 137 | 53 | 197 | 363 | 613 | 485 | 7,541 | 2,286 | 8,465 | 21,055 | 273 | 1,156 | 6 |
| Leopard | 50,469 | 41,737 | 55,371 | 65,826 | 75,695 | 69,187 | 101,309 | 70,666 | 49,380 | 40,085 | 26,966 | 34,956 | 22,267 | 14,590 |
| Thresher, Pelagic | 249 | 772 | 2,294 | 237 | 640 | | 10,923 | | | | | | | |
| Salmon | 351 | 268 | 255 | 2,252 | 2,016 | | 230 | 996 | | | | | 77 | |
| Sevengill | 13 | 21 | 170 | 55 | 893 | 282 | 1,735 | 2,041 | 3,415 | 545 | | 84 | | |
| Sixgill | 135 | 20 | 55 | | 4 | 96 | 128 | | 317 | 12 | 20 | | | |
| Hammerhead, Smooth | 158 | 537 | 1,807 | 3,628 | 3,920 | 6,831 | 44,481 | 1,866 | 2,259 | | 304 | 1,025 | 1,860 | |
| Soupfin | 170,834 | 146,595 | 227,690 | 197,164 | 243,661 | 558,280 | 176,155 | 249,070 | 257,348 | 192,119 | 221,840 | 176,070 | 162,166 | 182,390 |
| Spiny Dogfish | 6,502,244 | 7,498,128 | 8,140,022 | 5,153,659 | 5,534,759 | 7,653,279 | 5,398,472 | 4,593,164 | 4,832,581 | 7,141,589 | 9,562,516 | 6,476,814 | 5,813,829 | 5,831,992 |
| Swell | 4 | 2 | | | 20 | 222 | | | | 163 | | 2,795 | | |
| Great White | 1,312 | 2,196 | 1,343 | 923 | 2,861 | 6,102 | 634 | 8,052 | 42 | 1,660 | 2,269 | | | |
| Unspecified Shark | 30,024 | 46,670 | 177,339 | 135,146 | 193,317 | 181,373 | 181,373 | 273,721 | 580,932 | 1,158,219 | 840,956 | 600,473 | 563,382 | 582,450 |
| Total W.C. Sharks | 8,114,701 | 9,392,422 | 10,971,182 | 8,534,930 | 9,197,452 | 11,111,102 | 8,484,599 | 8,542,550 | 8,440,087 | 10,824,171 | 11,669,256 | 7,781,748 | 6,813,367 | 6,671,385 |

abundant shark species overall in the commercial catch have been the common thresher, shortfin mako (*Isurus oxyrinchus*), Pacific angel, soupfin, blue (*Prionace glauca*) and leopard sharks (*Triakis semifasciata*).

**Table 2. California commercial shark landings (in pounds)**

| Species | 1989 | 1988 | 1987 |
|---|---|---|---|
| Pacific angel | 268,252 | 491,348 | 940,187 |
| Thresher, bigeye | 22,093 | 12,033 | 25,305 |
| Blue | 13,621 | 7,147 | 3,410 |
| Mako, shortfin | 388,322 | 489,217 | 612,020 |
| Smoothound, brown | 10,967 | 15,522 | 12,916 |
| Thresher, common | 649,174 | 536,711 | 525,104 |
| Cow | 131 | 156 | 358 |
| Smoothound, grey | 412 | 20 | |
| Horn | 32 | 137 | 53 |
| Leopard | 50,469 | 41,737 | 55,371 |
| Thresher, Pelagic | 249 | 772 | 2,294 |
| Salmon | 351 | 268 | 255 |
| Sevengill | 13 | 21 | 170 |
| Sixgill | | 20 | 55 |
| Hammerhead, smooth | 158 | 537 | 1,807 |
| Soupfin | 166,305 | 140,566 | 201,489 |
| Spiny Dogfish | 3,430 | 3,789 | 53,935 |
| Swell | 4 | 2 | |
| Great White | 1,312 | 2,196 | 1,343 |
| Unspecified shark | 28,641 | 44,236 | 167,867 |
| Total sharks | 1,603,936 | 1,786,435 | 2,603,939 |
| Skate, unspecified | 168,511 | 127,861 | 169,712 |
| Stingray | | 36 | 298 |

All weights are unloaded weights. Only the smoothhounds, horn and spiny dogfish are landed round weight. All others are market dressed in the field.

California shark catches, while most diverse, have shown a consistent decline in the last three years (Table 2). Landings in 1987 were 2.6 million lbs (~1,812 MT), dominated by Pacific angel, shortfin mako, and common thresher sharks. By 1989, the landings were down to 1.6 million lbs (~727 MT), and those of the common thresher dominated, with Pacific angel and shortfin mako shark catches showing significant declines. Due to the shortfin mako longline fishery, their landings subsequently increased. The soupfin shark catch has remained fairly consistent, but spiny dogfish, which were fairly common in 1987, had much lower catches during the next two years.

The commercial shark catches in Oregon were much less diverse and lower in abundance than those in California (Table 3). There has been a major decline from the 123,045 lbs (~56 MT) landed in 1987, dominated by the common thresher shark, to only 7,500 lbs (~3.4 MT) in 1989, dominated by soupfin sharks, mainly because Oregon cancelled their experimental fishery.

**Table 3. Oregon commercial shark landings (in pounds)**

| Species | 1989 | 1988 | 1987 |
|---|---|---|---|
| Thresher, common | 30 | 88,957 | 101,664 |
| Sixgill | 135 | | |
| Soupfin | 3,265 | 3,029 | 17,511 |
| Spiny Dogfish | 698 | 1,110 | 225 |
| Unspecified, shark | 159 | 67 | 3,645 |
| Total sharks | 7,550 | 93,163 | 123,045 |

Off Washington there were only four species of sharks taken commercially, with the total annual catches remaining steady around 3.5 million lbs during the past three years (Table 4). Catches have always been dominated by spiny dogfish. The common thresher was commonly taken in 1987, but declined in the next two years.

**Table 4. Washington commercial shark landings (in pounds).**

| Species | 1989 | 1988 | 1987 |
|---|---|---|---|
| Blue | | 123 | 497 |
| Thresher, common | 5,874 | 14,105 | 143,324 |
| Soupfin | 1,264 | 3,000 | 8,690 |
| Spiny Dogfish | 3,123,546 | 3,520,296 | 3,466,706 |
| Unspecified, shark | 1,224 | 2,367 | 5,827 |
| Total sharks | 3,131,908 | 3,539,891 | 3,624,044 |

## The Spiny Dogfish Fishery

The spiny dogfish is one of the most abundant sharks in temperate waters around the world, and it has been an important commercial species in many areas of the world (Ketchen 1986, Hanchet 1988, Holts 1988). Over the past 13 years, catches have gone through radical changes, especially in Canadian waters (Table 5). In the middle 1970s, there was virtually no catch of spiny dogfish north of Washington, but catches have steadily increased from 1983 to the present. This has been paralleled by relatively consistent catches in Washington, which have varied from a peak year 9.4 million lbs (~4,273 MT) in 1979 to 3.1 million pounds (~1,409 MT) in 1989. Catches from Canadian waters but landed in the United States have paralled those from Washington. The catches from Oregon and California have never amounted to much (Table 5).

**Table 5. Spiny dogfish landings (in pounds) in Washington, Oregon andCaliforniafrom 1976 through 1989.**

| | Washington | | | Oregon | California | Total U.S. |
|---|---|---|---|---|---|---|
| | WA. Waters | Can. Waters | Total WA. | | | West Coast |
| 1989 | 3,123,546 | 3,374,570 | 6,498,116 | 698 | 3,430 | 6,502,244 |
| 1988 | 3,520,296 | 3,972,933 | 7,493,229 | 1,110 | 3,789 | 7,498,128 |
| 1987 | 3,466,706 | 4,619,156 | 8,085,862 | 225 | 53,935 | 8,140,022 |
| 1986 | 1,913,714 | 3,230,521 | 5,144,235 | 363 | 9,061 | 5,153,659 |
| 1985 | 2,837,927 | 2,839,863 | 5,677,790 | 290 | 1,002 | 5,679,082 |
| 1984 | 4,057,235 | 3,578,722 | 7,635,957 | | 17,181 | 7,653,138 |
| 1983 | 3,915,984 | 1,427,956 | 5,343,940 | | 54,532 | 5,398,472 |
| 1982 | 4,587,613 | | 4,587,613 | | 5,551 | 4,593,164 |
| 1981 | 4,542,064 | 275,671 | 4,817,735 | | 14,846 | 4,832,581 |
| 1980 | 7,069,171 | 57,138 | 7,126,309 | | 15,280 | 7,141,589 |
| 1979 | 9,435,004 | 10,000 | 9,445,004 | | 117,512 | 9,562,516 |
| 1978 | 6,031,300 | 5,511 | 6,036,811 | | 440,003 | 6,476,814 |
| 1977 | 5,428,652 | | 5,428,652 | | 384,177 | 5,812,829 |
| 1976 | 5,809,295 | | 5,809,295 | | 22,697 | 5,831,992 |

Historically, the spiny dogfish fishery has been subject to a "boom or bust" scenario (Anderson 1990). This may be due to its unique life history (Jones and Geen 1977; worldwide review in Hanchet 1988). It grows very slowly, lives a long time, has a very late age at first reproduction, low fecundity, and long gestation period, and is virtually absent from commercial fished areas for approximately the first 20 years of life. Without effort statistics, it is impossible to accurately depict what is happening to this population. However, it appears that it is commonly susceptible to overfishing, but that its longevity and absence from the fishery for much of its early life allows it to come back with vigor. Its present recovery is both a positive sign and a warning to carefully watch the north Pacific population.

## The Common Thresher Shark Fishery

The drift gill net fishery for common thresher sharks began developing off the southern California coast in the late 1970s. Market demand grew rapidly and the fishery was further stimulated by the more valuable by-catch of swordfish (*Xiphias gladius*) (Cailliet and Bedford 1983, Holts 1988). Despite several attempts to limit the fishery, it grew and expanded for several years. Swordfish became the primary target species and the number of vessels grew to over 200 by 1982. Each year after 1982 brought more northern expansion, first to Morro Bay, then Monterey and San Francisco, and ultimately to Oregon and Washington.

Common thresher shark landings peaked in 1982 at 2.4 million lbs (~1,091 MT, dressed weight) and then declined (Table 1, Figure 2). The coastwide fishery for this once abundant shark is now a thing of the past. It may be many years before stocks can support the demands of commercial exploitation.

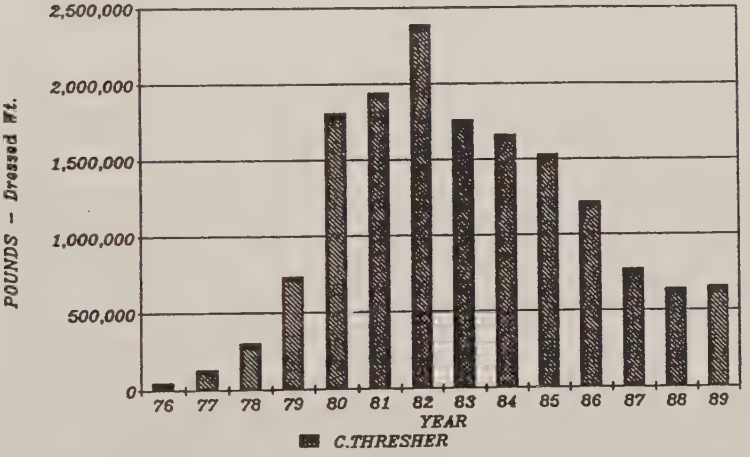

Fig. 2. Trends in annual west coast commercial common thresher (*Alopias vulpinus*) landings (in pounds, dressed weight) from 1976 through 1989.

Legislation passed in 1986 limited the directed common thresher shark fishery to 30 days during the month of May. Approximately 50 percent of the annual catch was taken during this period while the remainder was taken as a by-catch in the swordfish fishery during the fall and winter months. Small numbers of common thresher sharks were landed in Washington and Oregon during the mid-1980s, but declined drastically after 1988 (see Table 4). All directed fisheries for this species were terminated prior to the 1990 season and a tri-state management plan to limit the fishery was implemented in October, 1990. Common thresher sharks can still be taken and sold as a by-catch in the California drift gill net fishery for swordfish. While technically these sharks are not targetted during the swordfish season, nevertheless their landings are steady at about 0.6 million lbs (~273 MT) of one and two year old fish. However, only immature fish (averaging two years old) are taken (California Department of Fish and Game 1991).

### The Shortfin Mako Shark Fishery

Shortfin mako (=bonito) sharks were taken primarily as an incidental but valuable by-catch in the California drift gill net fishery for swordfish and thresher shark. Only a few individuals have ever been taken off Oregon and Washington. There are a couple of good reasons why the shortfin mako shark is, only now, becoming the primary target of a commercial longline fishery. Although readily marketable, they average only 34 lbs (~15.5 kg) dressed weight off southern California, compared to the 150 lb (~68 kg) average for common threshers in the late 1970s (Cailliet and Bedford 1983). Thus, the catch from both drift gill nets and longlines has been almost entirely composed of juveniles (one, two, and three year olds: California Department of Fish and Game 1991), although some mature adults were taken. As long as the threshers were plentiful, fishermen paid little attention to the shortfin mako.

Shortfin mako drift gill net catch rates peaked at 537,000 lbs (~244 MT) in 1982, and, following the common thresher shark fishery, declined to 215,000 lbs (~98 MT) by 1985 (Table 1, Figure 3). A few longline vessels began working the southern California Bight in 1986 and 1987. Landings increased but have subsequently declined to a level below 400,000 lbs (~182 MT). It took this entirely new fishing gear to create commercial interest in the shortfin mako shark.

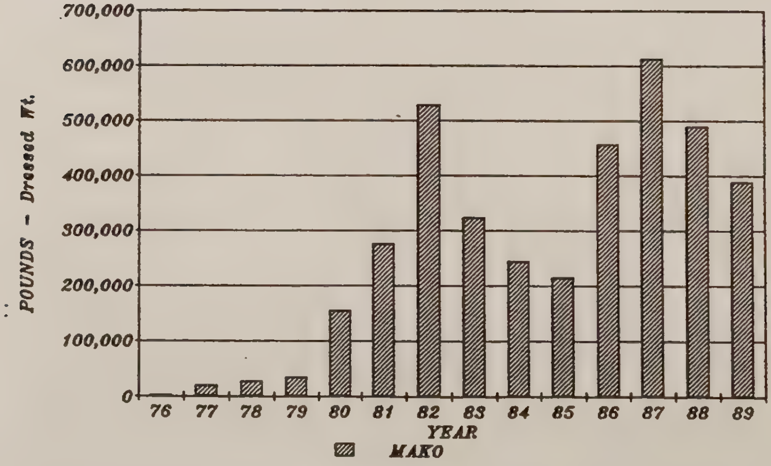

Fig. 3. Trends in annual west coast commercial bonito (= mako) shark *(Isurus oxyrinchus)* landings (in pounds, dressed weight) from 1976 through1989.

In 1988, the California Fish and Game Commission established an experimental, 10 vessel, longline shark fishery for shortfin mako and blue sharks. The gear is composed of a 3 to 4 mile (4.8 to 6.4 km) long stainless steel cable, to which leaders and baited hooks are attached. The entire cable is buoyed, at intervals of approximately 250-300 feet (75 to 90 m), so that the entire length of line remains in the near surface zone.

Continuation of this experimental fishery into 1990 required the most stringent regulations yet imposed on a shark fishery. These regulations stated that there will be: 1) only six (6) permits; 2) time/area closures away from sport fishing areas; 3) a total allowable landing quota set at 175,000 lbs (~80 MT); 4) a market developed to utilize the blue shark by-catch; and 5) a reduction of blue shark mortality. After three years, little progress has been made toward developing a market for blue shark. However, it has been demonstrated, beyond any doubt, that longlines are a potent gear for capturing mako sharks. During the first year of operation, the landings of approximately 240,000 pounds (~109 MT) were larger than the quota established later and equalled the entire "incidental catch," by the 250 vessel drift gill net fleet.

At some point during the mid-1980s, the shortfin mako shark captured the attention of the southern California sport fishing public as well. Surprisingly, prior to this time, little attention had been paid to it, even though these sharks have been long esteemed as game fish along the U.S. east coast. Between 1986 and 1989, estimates of the number of California angler trips for mako sharks grew ten fold, from 41,000 to over 410,000 trips annually. Commercial passenger fishing vessels ("party boats") now run shark fishing trips, on a regular basis, from nearly all southern California ports. The number of shortfin mako shark tournaments now takes second position, only to marlin tournaments, as southern California's most prestigious saltwater fishing event.

The experimental commercial long-line fishery was expected to continue on a year-to-year basis become California's first success at "resource stewardship" of an elasmobranch fishery. The 1990 season ended on September 30, 1990 with 175,000 lbs ((~80 MT) of shortfin mako shark landed. Blue shark mortality was reduced to near 22% and a small experimental market was established. In addition, the six permittees, in cooperation with the California Department of Fish and Game, reported tagging and releasing 600 shortfin mako sharks for distribution and abundance studies.

The shortfin mako shark population, like other oceanic sharks, is believed to be healthy, and relatively unexploited. Adults do not frequent California's coastal waters, and so are not subject to local fisheries. But a real threat to this shark population off California and elsewhere in the eastern Pacific lies in the potential for overexploitation by fisheries within the coastal "nursery" areas. This threat is particularly insidious, since the effect of over-fishing may not manifest itself for a number of years, until the missing juveniles would have themselves become the spawning stock. A sudden population collapse might follow. It appears that the lessons learned from the common thresher shark and others around the world inspired a far more conservative approach to this fishery's management, resulting in a denial by the California Fish and Game Commission for permits to continue the experimental drift longline fishery for shortfin mako sharks in 1992. In addition, in 1991 the Commission adopted specific bag limits (Section 27.60, Title 14, CCR) for the sport take of shortfin mako and five other species of sharks.

### The Blue Shark Fishery

Prior to the California experimental longline fishery, the only fishery directing effort at blue sharks occurred in 1979-1980 when one longline vessel fished for blue and shortfin mako sharks off southern California (Cailliet and Bedford 1983). The greatest source of fishing mortality for blue sharks occurred from their incidental capture during the developmental years of the drift gill net fishery off southern California. Preliminary annual mortality estimates were 15,000 to 20,000 sharks during that period. Changes in gear design and time-area closures reduced this incidental take, but there are no current mortality estimates for this fishery.

Only a portion of those taken by commercial fisheries are reported (Tables 1, 2, and 4), because there is virtually no commercial use yet developed for them, and most are discarded or used for fish meal. A small percentage of blue sharks are also taken in the set net fisheries for the Pacific angel shark and California halibut (*Paralichthys californicus*).

The current experimental longline fishery off southern California averages about four blue sharks for each shortfin mako shark. The fishermen in this fishery have reduced the incidental mortality of blue sharks through the development and use of a de-hooking tool (modified fence pliers) to remove the hooks from live sharks. Permittees are required to develop a market for the blue sharks not released in the by-catch. In 1989, 9,130 pounds (~4 MT) of blue shark were sold and an additional 43,000 pounds (~20 MT) sold in the 1990 season for jerky and for "fish and chips."

### The Angel Shark Set Net Fishery

A local fishery for angel sharks began developing in the Santa Barbara Channel during 1978 (Richards 1987). Initial marketing problems involved dressing the sharks at sea, which resulted in a 50% dressed landing weight of the live weight. There was an additional 50% loss at the fish market, with the net yield being 25-30%. The fishery expanded at an explosive rate as a result of more efficient processing procedures and new markets. These bottom dwelling sharks generally remain alive in the nets and small (< 42 inches or ~107 mm) individuals are returned to the sea in viable condition.

In 1985, the angel shark replaced the thresher shark as the principal food shark from southern California. Landings exceeded 1.2 million lbs (~546 MT) in both 1985 and 1986, but declined drastically by 1989 (Tables 1 and 2, Figure 4). This was a result of a combination of declining availability and alternative sources of low-cost imported shark meat.

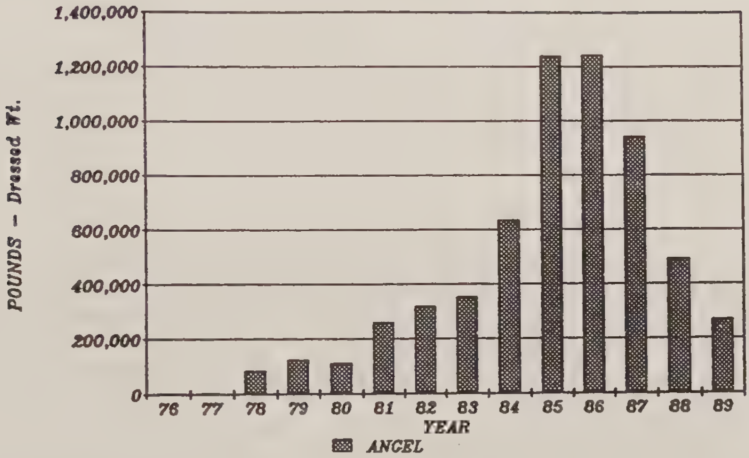

Fig. 4. Trends in annual west coast commercial angel shark (*Squatina californica*) landings (in pounds, dressed weight) from 1976 through 1989.

The most practical approach to take with this set net fishery was a minimum retention size limit, adopted in July 1988 (42 inches or 107 mm TL for females and 40 inches or 102 mm TL for males). Because the sharks caught are generally alive and hardy, release of undersized specimens would be a practical solution. Despite this management strategy, the continuation of a prosperous angel shark fishery did not occur. The major reasons for this include: 1) their lethargic and residental behavior; 2) their relatively low fecundity (Natanson and Cailliet 1986); 3) their apparently slow growth (Natanson and Cailliet 1990, Cailliet et al. 1992); 4) their demographic traits which make them susceptible to overfishing (Cailliet et al. 1992); and 5) the intensity of the set net fishery. However, as a result of Proposition 132, approved by California voters in 1990, set gill nets will not be allowed in nearshore waters, starting in 1994. Because fishermen must surrender their permits by 31 December 1993, this should effectively solve the problem of managing the Pacific angel shark fishery.

## The Soupfin Shark Fishery

More than 24 million lbs (~10,909 MT) of soupfin shark were landed from California waters in the eight years ending in 1944. This fishery decimated the soupfin population. A very small but consistent set net fishery for soupfin sharks has persisted over the past couple of decades. Landings in this fishery have roughly averaged between 150,000 and 250,000 lbs (68 to 114 MT: Table 1, Figure 5). It can be and has been a target for commercial fishermen, but is most often taken incidental to other commercial species.

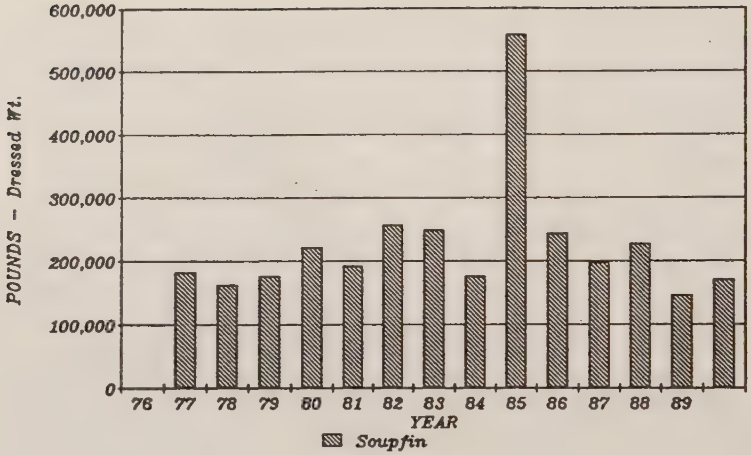

Fig. 5. Trends in annual west coast commercial soupfin shark *(Galeorhinus zyopterus [=galeus])* landings (in pounds, dressed weight) from 1977 through 1989.

## The Leopard Shark Fishery

The leopard shark (*Triakis semifasciata*), another common inshore species, is fished both recreationally, mainly by hook and line, and commercially, usually as a by-catch of other net fisheries (Smith and Abramson 1990). Its west coast landings have fluctuated from a low of 14,590 lbs (~7 MT) in 1976, to a high of over 100,000 lbs (~45 MT) in 1983 (Table 1, Figure 6).

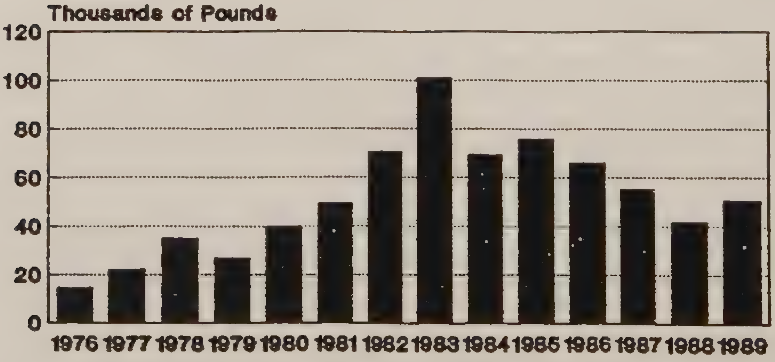

Fig. 6. Trends in annual west coast commercial leopard shark *(Triakis semifasciatus)* landings (in pounds, dressed weight) from 1977 through 1989.

Although there has been a general decline since then, there is no immediate reason for concern if growth, natural and fishing mortality, and demography estimates (Smith and Abramson 1990; Kusher et al. 1992; Cailliet 1992) are correct. Even so, the California Fish and Game Commission in 1991 adopted a minimum size (36 inches or 981 mm TL) and a bag limit (three per fisherman) for recreational anglers.

### Management Strategies for Elasmobranch Fisheries

It is a tragedy of unsound resource management that it took an obvious decline in fishing success for both common thresher and angel sharks in California to finally prompt the state to adopt serious regulations. Unfortunately, throughout the history of shark fisheries, this is a common mistake, repeated again and again. Resource managers need to understand more basically the unique limitations imposed by the life histories of sharks and rays, so they can convince those who make and enforce the regulations that such fisheries need to be seriously limited.

Several recent actions in California and the other western U.S. states are promising. The initiation of the experimental longline fishery in 1990 for shortfin mako and blue sharks was accompanied by the strict regulations already described, including a limited number of permits, time/area closures away from sport fishing areas, a landings quota, development of a market for the blue shark by-catch, and a reduction of blue shark mortality. The California Fish and Game Commission's authority to authorize experimental fisheries was given to it by the legislature and intended to develop new fisheries, either by gear or species target changes. Experimental fisheries were never intended to perpetuate limited commercial fisheries. At some point, each experiment is declared a success or failure. If it is characterized as a success, the legislature can authorize a new commercial fishery. As mentioned, the experimental longline fishery for shortfin mako sharks was closed in 1992.

Also, approval of Proposition 132 in November, 1990 will limit the use of set gill nets inside three miles of the California coast and will consequently affect the fisheries for (and thus landings of) soupfin, Pacific angel and leopard sharks. Common thresher, blue, shortfin mako, and soupfin sharks, caught by drift gill nets, will not be affected by this law.

Management options in general for elasmobranch fisheries include:

1) no restrictions at all (ultimately an economic solution);
2) limited entry of fishermen and vessels into the fishery;
3) size limits; 3) bag limits;
4) closed areas and/or seasons;
5) quotas;
6) gear restrictions; and/or
7) closure or total shutdown of the fishery.

All of these measures have advantages and disadvantages relative to the particular fisheries in question.

Having no restrictions at all leads to the rapid decline of most elasmobranch populations, resulting in a wide-scale decimation of some major predator populations and possibly altering the ecosystems in which they operate. This option, although apparently the one most often used, is not a viable alternative.

Limited entry is a viable option if the fishery has not already developed a large fleet. Unfortunately, once the threat to a fishery is evident, it is usually too late to limit the number of fishermen or vessels allowed to use the resource. This approach is costly, both monetarily and legally, and should be considered only if all other possible approaches prove ineffective.

Size limits are valuable in that they can influence the age at entry into fishery, and thus have a major impact on the proportion of reproductively viable individuals subject to fishing mortality. This approach requires valid life history information such as age (Cailliet 1990, Cailliet et al. 1986), growth (Cailliet and Tanaka 1990), age composition, age-specific mortality, age-at-maturity, and age-specific natality (Pratt and Otake, 1990), which often provides demographic information (Cailliet 1992, Cailliet et al. 1992). These approaches are often costly and have not been used on many elasmobranch species, mainly because the life history information is unavailable (Cailliet 1990). Also, some gears (i.e. drift gill nets) do not allow for the live release of undersized fish.

However, with this information, fishery regulations can insure, either via logistic, dynamic pool, or demographic models (Hoenig and Gruber 1990), the continued stable existence of a fished stock. Unfortunately, this approach has only been used on a few elasmobranchs which support fisheries (Jones and Geen 1977, Grant et al. 1979, Ketchen 1986, Anderson 1990, Smith and Abramson 1990, Cailliet 1992, Cailliet et al. 1992).

Catch limits basically are strongly tied to the number of fishermen utilizing the resource. This approach also requires detailed life history information, especially good estimates of population size, and therefore can be expensive. It is very difficult to enforce and is used primarily in sport fisheries. In fact, as mentioned earlier, the California Fish and Game Commission in 1991 adopted specific bag limits for the sport take of shortfin mako, along with thresher, soupfin, sixgill (*Hexanchus griseus*), sevengill (*Notorhynchus cepedianus*) and leopard sharks.

Closed areas and seasons have been used with some success in California shark fisheries (Bedford 1987, Richards 1987, Holts 1988). This is usually the most successful when movement patterns or important life processes (reproduction, spawning, larval or juvenile growth, feeding, etc.) occur in a specific place at a specific time, and the fishery can be directed away from these. In most cases, however, these details are not well known for elasmobranch fishes subject to fishing pressure.

Quotas are another management approach and these have been used in only one shark fishery, the shortfin mako, in which a new gear was being used and evaluated. It is too early to determine whether this approach has been successful. To set quotas, a great deal of knowledge of the life history of the species involved is required. This approach has been used extensively for northeast Pacific fisheries to regulate groundfish catches. It often involves some equation, based upon maximum or optimum sustainable yield (MSY or OSY) estimates from extensive catch data collection and analysis, which leads to the total allowable catch (TAC) and can be revised from year to year, depending on future catch statistics. The use of fisheries models on elasmobranch populations is reviewed by Anderson (1990).

The final two approaches, gear restrictions and closure or shutdown of a fishery, may be the only viable one for some elasmobranch fisheries. It is hoped, however, that intelligent data gathering and decision making will occur prior to implementating these radical solutions.

### Acknowledgements

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# EFFECTS OF THE STIPE-BORING AMPHIPOD *PERAMPHITHOE STYPOTRUPETES* (COROPHIOIDEA: AMPITHOIDAE) AND GRAZING GASTROPODS ON THE KELP *LAMINARIA SETCHELLII*

*J. R. Chess*

## ABSTRACT

The ampithoid amphipod *Peramphithoe stypotrupetes* hollows and infests the stipes of the alga *Laminaria setchellii* after intense grazing of its lamina by gastropods. The intensity of gastropod grazing and subsequent levels of amphipod infestation appear to be correlated with calm ocean conditions. Once established in the stipe, a pair of adult amphipods produces multiple cohorts of offspring, which hollow and kill the plant. At a study site off northern California, an entire bed of the alga was infested and no plants survived. Aspects of the natural history of *P. stypotrupetes* are discussed.

Invertebrates that graze on the mature sporophytes of large brown algae (kelps) generally cause only minor damage to the plants (Foster and Schiel, 1985), but there are exceptions. The decimation of kelp forests by echinoids has been well documented (e.g., Lawrence, 1975; Chapman, 1981), but many of these occurrences are believed to be unnatural events that are the result of population explosions stimulated by coastal pollution or the lack of natural predators (North and Pearse, 1970; Estes and Palmisano, 1974; Kain, 1979). Natural population levels of sea urchins commonly have little effect on mature, attached kelp, since the urchins feed mostly on drift material (Foster and Schiel, 1985).

A number of mollusks and crustaceans are known to feed on kelps, but generally they are nonlethal. The European acmaeid *Patina pellucida* (L.) can graze and weaken the holdfast of *Laminaria hyperborea* (Gunn.) Foslie (see Kain, 1963), and the Californian trochids (*Tegula* spp.) can damage kelp lamina when numerous (Foster and Schiel, 1985; personal observation). Other gastropods are damaging only when in abnormally high densities, as, for example, *Lacuna vincta* (Montagu), which can markedly deplete stands of *Laminaria saccharina* (L.) (see Fralick *et al.*, 1974). Crustaceans that burrow into stipes and holdfasts of kelp, usually with nonlethal effects, include the isopods *Limnoria algarum* Menzies and the amphipod *Ampitholina cuniculus* (Stebbing), as well as members of the amphipod families Biancolinidae, Najnidae, Phliantidae, and Eophliantidae (Menzies, 1957; Myers, 1974; Conlan and Chess, 1992).

Members of the herbivorous corophioidean amphipod family Ampithoidae inhabit self-constructed tubes or chambers in coastal marine algae (Conlan and Bousfield, 1982). Among these, certain species of *Peramphithoe* have developed a partially close relationship with brown algae of the order Laminariales on which they live and feed. *Peramphithoe humeralis* (Stimpson) in the northeastern Pacific and *P. femorata* (Krøyer) in the southeastern Pacific both inhabit *Macrocystis pyrifera* (L.), where they fold and stitch (glue) lamina margins into chambers (Limbaugh, 1955; Kreibolm de Paternoster and Escofet, 1976). Although these species graze the lamina, they are not fatal to the plants.

In the northeastern Pacific, *Peramphithoe stypotrupetes* Conlan and Chess hollows and inhabits the stipes of *Eisenia arborea* Areschoug and *Laminaria setchellii* (see Conlan and Chess, 1992: *L. setchellii* Silva as *L. dentigera* Kjellman). This relationship appears to be unique, in that the alga is almost always destroyed, the destruction sometimes involving entire beds. The amphipod feeds on the medullary and cortical tissues of stipes, forming a hollowed chamber where a pair of adults, and their successive broods, feed and grow, eventually causing the death of the plant (Conlan and Chess, 1992). This report describes how *P. stypotrupetes* infests *L. setchellii*, documents its impact, and presents additional natural history observations to those reported in Conlan and Chess (1992).

## Study Areas

Observations and collections were made irregularly between 1972 and 1992 during other investigations along the Mendocino coast of northern California (39°21′N, 123°50′W), Baranof Island (56°03′N, 134°20′W), southeastern Alaska, and off Santa Catalina Island (33°28′N, 118°29′W), southern California. Directed studies on the infestation by *Peramphithoe stypotrupetes* and attrition rates of *Laminaria setchellii* were made at Pt. Cabrillo on the Mendocino coast between November 1978 and April 1981, but other observations came from the various sites along that coast throughout the 20-year period.

Pt. Cabrillo, a state biological preserve, is an exposed rock headland with surge channels 3–20 m in depth that are semi-protected from moderate seas by offshore reefs and exposed rocks. The fauna and flora are typical of a northern California wave-swept habitat, with the most conspicuous kelps being *Postelsia palmaeformis* Ruprecht and *Lessoniopsis littoralis* (Tilden) in the intertidal, *Laminaria setchellii* from the lower intertidal to about 10-m depth, and *Pterygophora californica* Ruprecht and *Nereocystis leutkeana* Mertens growing from depths of about 8–15 m. The area observed encompassed approximately 1,200 $m^2$.

## Incidental Observations

The association between *Peramphithoe stypotrupetes* and kelps was first recognized in 1972 at Santa Catalina Island, where abraded stipes of *Eisenia arborea* were collected and noted to contain numerous ampithoid amphipods. The same condition was observed in the stipes of *Laminaria setchellii* in northern California in 1977, and in Alaska during 1980.

Successful stipe infestation by the amphipods appeared to depend upon initial intense grazing by other invertebrates on lamina tissues and to some extent the transition zone (the main region of active cell division, located between the stipe and lamina). If the meristem in the transition zone is destroyed, then the plant is incapable of further growth and dies (Kain, 1971).

Along the Mendocino coast, infested stipes were conspicuous during most years. However, the highest rates of infestation appeared to coincide with years of exceptionally calm fall and winter months. Observations during these calm periods revealed an unusually high degree of grazing on the lamina of *L. setchellii* by benthic herbivores, primarily gastropods (Fig. 1). The grazers concentrated on the perennial kelps during the winter months when ephemeral algae were scarce or absent. The trochid gastropods *Tegula pulligo* (Gmelin), and, to a lesser extent *Calliostoma ligatum* (Gould), were the most prominent grazers during daylight hours. At night, other molluscan grazers became active, as evidenced by observations made in a quiet cove (Little River) about 8 km south of Pt. Cabrillo in March 1984. There, about two h after sunset, the trochids on the stipes and lamina of *L. setchellii* and *Pterygophora californica* were joined by several diurnally sedentary grazers, including the abalones *Haliotis rufescens* Swainson and *H. walallensis* Stearns and the chiton *Cryptochiton stelleri* (Middendorff).

These grazing molluscs appear to have limits to their ability to maintain a footing on stipes that are whipped by surge. It was noted that, under conditions of moderate surge (seas 1.5–2.0 m), trochids were absent from *L. setchellii* at depths shallower than about 7 m, but were present on those in adjacent sites at depths of 12–15 m. Under conditions of heavy surge, these gastropods appeared unable to maintain their position on stipe tips or lamina at any depth.

On the Mendocino coast, annual transition-zone expansion and lamina growth begins during late February and early March. Growth proceeds in the manner typical of other species of *Laminaria,* where "As the new lamina enlarges, the old one becomes a mere appendage at its apex and ultimately breaks off completely" (Fritsch, 1945, p. 195).

During early March (1992) at Mendocino, many *Tegula pulligo* and *Calliostoma ligatum* were observed feeding on the old lamina tissue, but not on the adjacent new growth of expanding lamina tissue (Fig. 2). This suggests that snail-induced damage to the transition zone takes place before the new growth begins, and that the damage is probably not lethal to the plant.

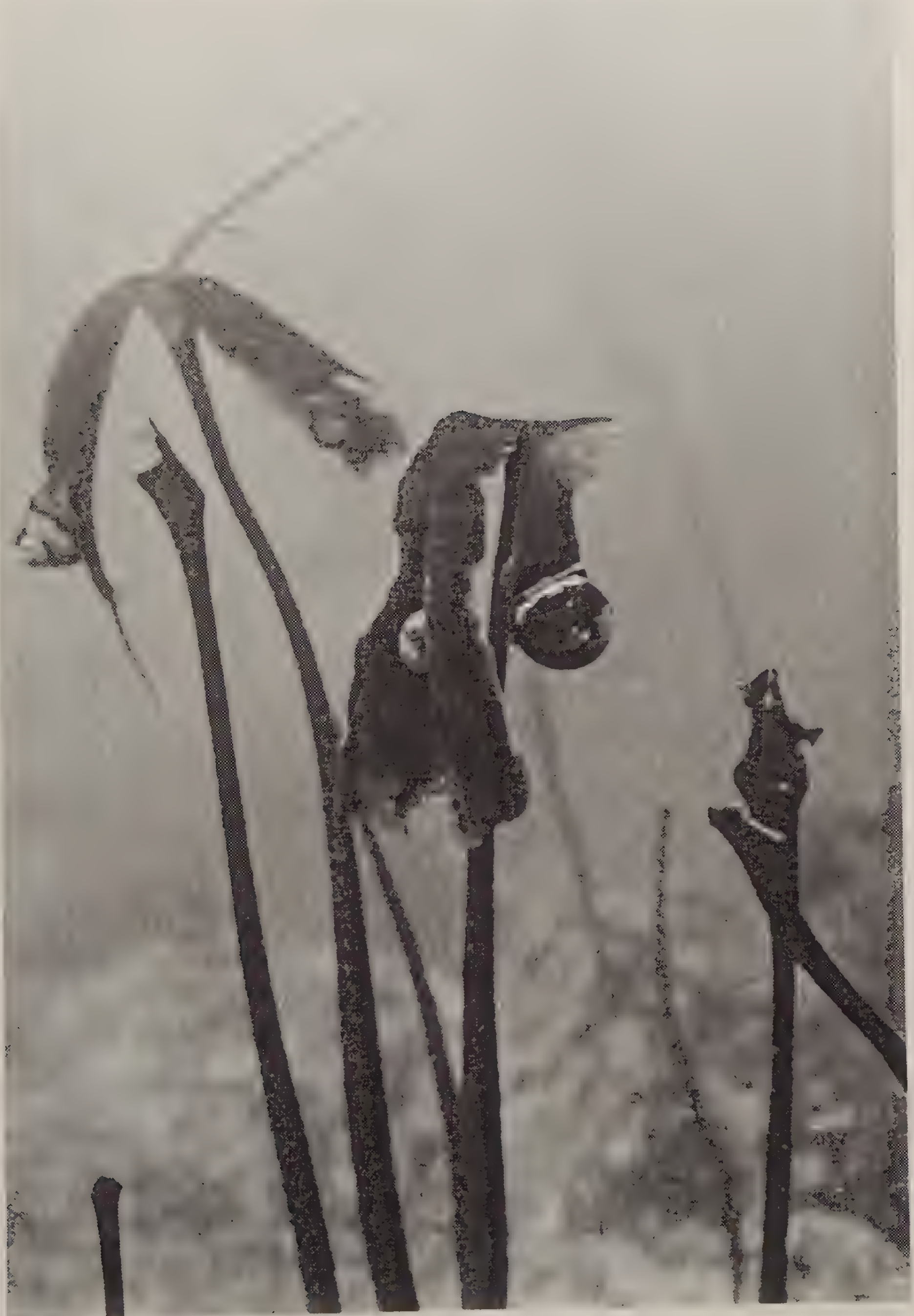

Fig. 1. *Tegula pulligo* grazing the lamina of *Laminaria setchellii* during a calm winter period (December).

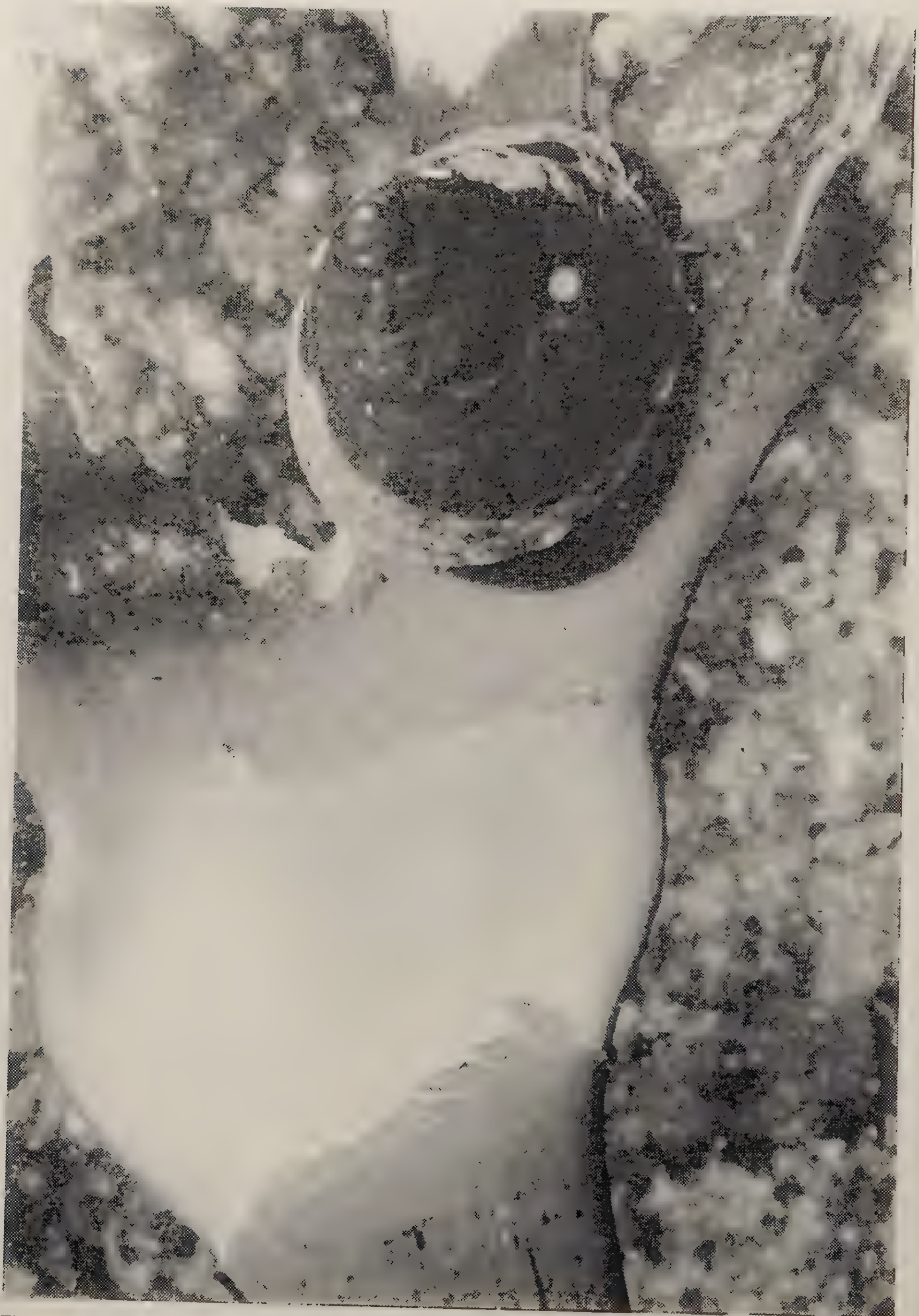

Fig. 2. Expanding new lamina (light area) in *Laminaria setchellii* with *Tegula pulligo* feeding on old lamina tissue during early spring (March).

All infestations of *L. setchellii* by *P. stypotrupetes* occurred on stipes that had lost lamina. However, stipes with the gastropod *T. pulligo* still attached often were grazed into the distal areas of the transition zone, whereas those abraded by physical forces retained at least a remnant of lamina and an intact transition zone. It appeared that only the gastropod grazers removed entire lamina, thus exposing stipe tissues to amphipod infestation.

## MATERIALS AND METHODS

Directed observations and measurements of the effects of *P. stypotrupetes* on *L. setchellii* were initiated at the Pt. Cabrillo site during 1978, and monitored irregularly until 1981. This site was assessed occasionally during the following years.

All field observations and collections were made using scuba or snorkel. At Pt. Cabrillo, individual plants of *L. setchellii* were marked with numbered disc tags in order to determine rates of infestation by the amphipod and stipe longevity after infestation. Stipes were measured (to the nearest 0.5 cm) from the base of the holdfast to the distal tip of the stipe. Collections of amphipods were made by severing infested stipes near the base, placing each stipe in a separate plastic bag and sealing with rubber bands.

## RESULTS

### Infestation by the Amphipod

During the fall and winter of 1978–1979 infestations became rampant when particularly calm ocean conditions prevailed from September through April.

*Laminaria setchellii* occurring in the shallowest depths appeared considerably healthier and less infested with the amphipod than those at greater depths. This relationship was measured during August 1980 at Pt. Cabrillo, when infested and healthy plants were tallied within depth-stratified, adjacent 1 × 25-m belt transects at depths of 1–2 m, 2–3 m, and 3–4 m on a vertical face of a deep surge channel. Within the shallow belt, 5 of 386 stipes (1.3%) were infested, and within the middepth, 12 of 54 (22.2%) were infested. In the deepest belt, only 2 bored-out stipe stumps and no intact plants were found.

Two groups of healthy, uninfested plants were tagged to determine rates of infestation. One group of 14 stipes (on an isolated boulder at a depth of 3 m) was tagged on 16 November 1978. Seven months later, one stipe was infested and five others were missing. After another 14 months, four more plants were infested, and the one infested earlier was a mere stump. Thus, after 21 months, only four of the original 14 plants remained uninfested. A group of 29 stipes in a surge channel at 2–4-m depth was tagged on 3 July 1979. Fourteen months later all 11 that remained were infested, and after another eight months no remnants of these plants remained. During subsequent observations in 1983 and 1985, no *L. setchellii* could be found in the study area, and by 1990 only a few plants with approximately 1-cm diameter stipes were present.

Throughout the study period, infested stipes were common and sometimes abundant at other sites along the Mendocino coast, but nowhere was the destruction of *L. setchellii* as severe as that observed at Pt. Cabrillo.

### Deterioration of Infested Stipes

Individual stipes varied considerably in their degree of infestation or deterioration. The most recently infested contained only one or two adult amphipods in excavations only a few cm deep, while adjacent stipes, apparently infested earlier, were severely damaged with tattered tips and perforations through the outer wall (Fig. 3). It was impossible to determine the number of amphipods in residence or the depth of the excavations in the more severely damaged stipes without dissecting them. However, as noted earlier (Conlan and Chess, 1992), the larger stipes with large chambers generally contained the most amphipods (Fig. 3). Nine of 11 infested stipes, tagged and measured along with the 14 healthy plants during November 1978, persisted for seven months before being remeasured in June 1979. Initially these plants varied in length from 33–55 cm ($\bar{x} = 46.3$ cm) and during the period were reduced to between 6 and 41 cm ($\bar{x} = 22.8$ cm), a mean rate of stipe reduction of 3.01 cm/month. The largest of the infested stipes (55 cm) was reduced at the greatest rate (6.71 cm/month), and the smallest at the lowest rate (1.10 cm/month), but this relation did not hold with intermediate-sized plants. The deterioration rate of the second (surge channel) group of stipes was not calculated, because it was not known when they had become infested.

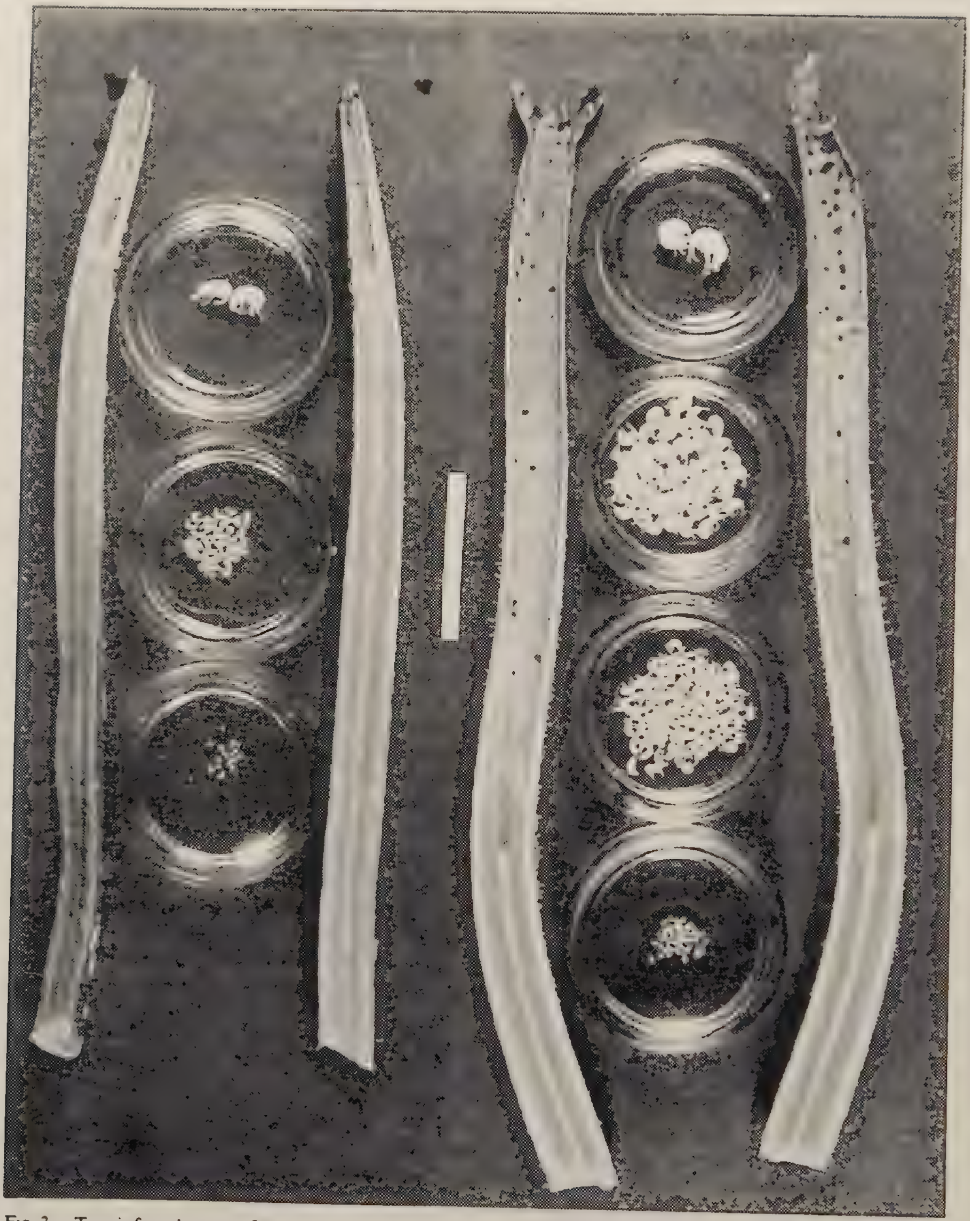

Fig. 3. Two infested stipes of *Laminaria setchellii*, the larger with lateral perforations, each with its complement of adults and offspring cohorts of *Peramphithoe stypotrupetes*, both collected 27 February 1992. (Scale bar = 5 cm; small chamber 6 cm long, larger 24 cm.)

## Amphipod Reproduction Within Stipe Chambers

Brooding females were found within infested stipes during all seasons. The size of brood or number of offspring within cohorts was variable, with the largest females tending to have the most and the smallest the fewest. Fecundity of females 20–24 mm in length ($N = 3$) was 85–145, $\bar{x} = 111.0$; among those 16–19 mm ($N = 8$) was 30–120, $\bar{x} = 69.0$; and from those 14–15 mm ($N = 2$) was 33–60, $\bar{x} = 46.5$. The smallest brooding female found was 14 mm. There appeared to be some mortality or loss of members of any cohort, as suggested by the numerical composition of those found in the large stipe of Fig. 3. Here, the number of offspring in three cohorts of a 19-mm female and 18-mm male were: 62 individuals in the 1.7–2.0-mm cohort, 94 at 5.5–7.0 mm; and 58 at 9–11 mm. The mother was carrying 120 embryos.

The number of cohorts cohabiting a chamber was positively correlated with the length of the hollowed stipe chamber. Offspring cohorts in chambers 2–4-cm long ($N = 7$) varied from zero–one, $\bar{x} = 0.29$; those from 5–10-cm chambers ($N = 13$) varied from zero–3, $\bar{x} = 1.23$. All chambers from 15–25 cm ($N = 5$) contained four cohorts, and the largest chamber observed, 116 cm, contained four or possibly five. Separating large individuals into cohorts was often difficult, because older amphipods appear to grow at a slower rate and their size groupings become more obscure. When the cohort size-classes were easily distinguished, the smallest were always found in the lowermost part of the chamber.

Several stipes that were variably hollowed out and decomposing contained no amphipods, and others that had been reduced to mere stumps (<10 cm high) often harbored only a few *P. stypotrupetes* of mixed sizes, and at times other species of gammarideans as well.

## Discussion

*Peramphithoe stypotrupetes* appears to be one of the few crustaceans known to be capable of large-scale killing of mature kelp sporophytes. However, other gammaridean amphipods, primarily *Peramphithoe humeralis*, have been described inflicting considerable damage to large areas of a forest of *Macrocystis pyrifera* off San Diego following a period of elevated sea temperatures (Tegner and Dayton, 1987). *Amphitholina cuniculus* burrows into the medullary region of the stipes of *Alaria esculenta* off Ireland (Myers, 1974). It was reported to have infested up to 82% of a bed of *A. esculenta* with a large proportion "so badly damaged . . . that it was unlikely that the alga would survive the winter" (Lewis, in Myers, 1974, p. 469). *Amphitholina cuniculus,* which is morphologically highly modified for burrowing (Conlan and Chess, 1992), enters the stipe laterally rather than through an abraded or grazed distal end as does *P. stypotrupetes* (see Myers, 1974).

### Conditions for Infestation

The relationship between increased grazing by gastropods on off-bottom kelp lamina and low water turbulence is probably wide spread. The brown sea hare *Aplysia californica* Cooper has been seen on the tops of *Pterygophora californica* when seas were calm (Foster and Schiel, 1985), and a one-day period of heavy surge dislodged all *Norrisia norrisi* Sowerby and *Tegula aureotincta* Forbes from the upper portions of plants of *M. pyrifera* (see Bakus, unpublished, cited in Lowry *et al.*, 1974). Surge from wave action is considered to be maximal in the subtidal fringe and to decrease gradually with depth, and the vertical distribution of many organisms is determined chiefly by these forces (Kitching, 1941). The reported observations thus indicate that less turbulent conditions in deeper water have allowed more intense gastropod grazing pressure on *L. setchellii,* and subsequently higher levels of infestation by *P. stypotrupetes,* than for plants at shallower depths. The extended period of calm ocean conditions during the fall and winter of 1978–1979, with intense gastropod grazing even at shallow depths, was probably the primary cause of the high level of stipe infestation and subsequent decline of the populations of *L. setchellii* at Pt. Cabrillo.

The relative tenderness of lamina tissue, as compared to the stipe and holdfast, may account for its apparent preference by grazing gastropods. Steinberg (1985) suggested that "stipes and holdfasts . . . are often much tougher than the blades of the same plant and that many herbivores, including *Tegula,* probably find it physically very difficult to consume these plant parts."

The avoidance of the newly expanding transition zones and laminae by gastropod grazers observed during March 1992 suggests that these tissues may produce higher levels of herbivore-deterrent chemicals than the older, degraded lamina. In studies of food preference, species of phaeophytes with high levels of phenolic compounds were avoided by *Tegula funebralis* (A. Adams), while those with low levels were preferred (Steinberg, 1985). In other studies, it was found that the young growing tips and reproductive structures of tropical green algae contained higher concentrations of noxious compounds than mature plant tissues (Paul and Fenical, 1986; Paul and Van Alstyne, 1988). A similar condition may exist with the new spring growth in *Laminaria*. It is also possible that trochid gastropods are incapable of maintaining a footing on the slippery new surfaces. Kain (1971) suggested that this "highly mucilaginous surface is not a very hospitable substratum for most organisms."

Avoidance of the new growth by gastropods suggests that whatever damage they cause to the lamina and distal transition zone must occur prior to new growth during the fall and winter months. Therefore, it seems unlikely that *P. stypotrupetes* could successfully invade stipes of *L. setchellii* during early spring and summer, when rapid lamina growth is in progress.

### Amphipod Infestation

The infestation of only those stipes of *L. setchellii* that have been previously grazed to or into the transition zone indicates that *P. stypotrupetes* is probably incapable of penetrating, or possibly using, the tissues of the lamina or outer stipe. The amphipod is, however, capable of entering and using the tissues of the transition zone and inner stipe, as the gut contents showed (Conlan and Chess, 1992).

In the Monterey Bay area, an ampithoid gammaridean, probably referable to *P. stypotrupetes,* was described as burrowing into the sides of stipes of *Pterygophora californica* (much as *Amphitholina cuniculus* enters *Alaria esculenta* (L.)), hollowing a chamber in the interior and producing successive broods of offspring. Mortality to these plants occurred when surge-induced turbulence broke the stipe off at the area of the chamber. Infestation levels were described as variable, at times as high as 20%, but at other times none could be found (Michael Foster, Moss Landing Marine Laboratories, personal communication, 24 March 1992). Schroeter (cited in Conlan and Chess, 1992) found this same relationship occurring off the coast of Santa Barbara. Although *P. californica* is a major component of the sublittoral off the Mendocino coast, there was no evidence of it being infested there, but it could easily have been overlooked if infestations occur infrequently or at low levels.

Hollowing of stipes of *Laminaria setchellii* by *Peramphithoe stypotrupetes* and the subsequent rate of stipe shortening undoubtedly accelerates with the development, growth, and increased feeding of successive broods. The mean rate of shortening (3.01 cm/month) would be much lower during initial infestation and much higher during later stages, the rate probably being proportional to the cumulative biomass of amphipods occupying a chamber.

The tendency for the crowded amphipods to perforate the distal portions of stipe chambers would allow increased water circulation inside, and thus enhance respiration and waste removal. It is unknown if the perforations are formed specifically or are simply the result of heavy grazing on the interior of the stipe. In either case, lateral stipe perforations would seem beneficial to amphipods occurring in high densities. However, the loss of a fraction of newly hatched juveniles, suggested above, may be proportional to the number of perforations present. On the other hand, the strong tendency of offspring cohorts to segregate by size (the smallest occurring deepest in the chambers where there are no perforations) must offset their potential loss.

The circumstances that stimulate the amphipod's abandonment of stipes is unknown, but is most likely related to the lack of available food, when the inner stipe tissues are gone, or to the noxious environment of the chamber when the remaining tissues begin to decompose. The length of time for the death of stipe tissue to occur and for decomposition to begin seems quite long, since actively infested stipes persisted for at least 223 days.

It appears that, for high levels of infestation to occur, extended periods of calm ocean conditions, coupled with extensive lamina grazing by gastropods, are required to permit the invasion of stipes by *Peramphithoe stypotrupetes.* At Pt. Cabrillo the infestation of stipes seemed to increase nearly exponentially during the 1978–1980 period. This was probably caused by rapid infestation of neighboring stipes by offspring of the initial invaders.

The original shallow-water community of *Laminaria* at Pt. Cabrillo was dramatically modified by the mortalities caused by the gastropod—*P. stypotrupetes* invasion. Although there have been subsequent low levels of recruitment, *L. setchellii* remains a minor component of the biota there after 12 years. However, at various sites in the vicinity of Pt. Cabrillo, *L. setchellii* is abundant and luxuriant. The situation at Pt. Cabrillo may be explained by its being a biological preserve where unusually high densities of the red abalone *Haliotis rufescens* occur. Although this abalone relies primarily on drift algae for nutrition (Leighton, 1971), intense grazing by these herbivores has probably precluded the reestablishment of *L. setchellii*. Even though plants of *L. setchellii* were virtually eliminated at Pt. Cabrillo, *P. stypotrupetes* appears to have little lasting effect on the structure of algal communities over time.

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# Comparison of age at sexual maturity and other reproductive parameters for two stocks of spotted dolphin, *Stenella attenuata*

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**Abstract.**–We examined the average age at attainment of sexual maturity (ASM) and several other reproductive parameters for evidence of density compensatory responses in two stocks of the spotted dolphin, *Stenella attenuata*. The northern offshore and southern offshore stocks were compared because both have been exploited by the yellowfin tuna purse-seine fishery, but at different rates. We predicted decreasing trends in the ASM and increasing trends in the pregnancy rate for each stock because both have declined in abundance. A lower ASM and a higher pregnancy rate were predicted for the sample from the northern offshore stock because it has been exploited to a greater extent than the southern offshore stock. No statistically significant trends were found in the ASM, but the increase in the proportion of sexually mature females simultaneously pregnant and lactating for the northern offshore stock and the decrease in the proportion of mature females in the population for the southern offshore stock over time were statistically significant. The mean estimate of ASM was significantly higher for the northern offshore stock, 11.1 years (SE=0.236), than for the southern offshore stock, 9.8 years (SE=0.264). No significant differences between stocks were found in the mean estimates of reproductive parameters. Our analyses of temporal trends in several biological parameters did not provide conclusive evidence for compensatory responses having occurred, and therefore some possible explanations are considered.

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As population abundance declines, compensatory responses, such as increases in survival and pregnancy rates and a decrease in the average age at attainment of sexual maturity (ASM), are thought to occur (Eberhardt, 1977; Eberhardt and Siniff, 1977). Each situation must be carefully evaluated to determine whether compensatory responses will be detected because the magnitude of the parameter response and the range of population densities over which measurements are made are likely to be species specific, environmentally variable, and subject to parameter measurement error (Goodman, 1981; Fowler, 1981, 1988; DeMaster, 1984a; York, 1987). For species that are difficult to observe, unbiased estimates of survival rates are difficult to obtain, precluding their use as potential biological indices (Barlow and Boveng, 1991). Reproductive rates, however, are generally more easily measured and, if their relationship to population density is determined, may provide indices of compensatory responses for populations (Perrin and Donovan, 1984). For instance, Barlow (1985) reported that in the spotted dolphin (*Stenella attenuata*), the fraction of mature females pregnant, and the fraction of mature females simultaneously pregnant and lactating, may correlate well with per capita resource availability because these parameters were found to be relatively free of collection biases. The identification of biological indices (i.e., biological parameters that correlate with population abundance) would provide a useful management tool to distinguish between trends in population abundance resulting from exploitation or changes in environmental conditions (Hanks, 1981; Gerrodette and DeMaster, 1990).

The spotted dolphin is an ideal choice for this analysis because a lengthy time series of biological and population abundance data are available. This species is used as a cue by purse-seine vessel operators to find yellowfin tuna in the eastern tropical Pacific (ETP) (Perrin, 1969). Dolphins are incidentally killed during fishing operations, and the spotted dolphin population has had the largest number of animals killed in almost every year since 1959 (Smith, 1983; DeMaster et al., 1992). Two stocks of spotted dolphin, the northern offshore and southern offshore stocks, are recognized as separate management units in the ETP (Perrin et al., 1985). During the first decade of the purse-seine fishery, the 1960's, the large numbers of dolphins killed caused the abundance of these two stocks to decline. The northern offshore spotted dolphin was estimated to be between 35% and 50% of their pre-exploitation abundance (circa 1959) by 1979 (Smith, 1983), while the southern offshore stock was estimated to be at 92–98% of its pre-exploitation size (circa 1973) in 1979 (Smith[1]). Since 1976, both stocks of spotted dolphin are believed to have declined significantly in abundance (Anganuzzi et al., 1992).

As potential biological indices, we estimated ASM and associated reproductive parameters for two stocks of the spotted dolphin. Although for long-lived mammals, like the spotted dolphin, population growth rates are relatively insensitive to changes in ASM and reproductive rates (Eberhardt and Siniff, 1977; Fowler, 1981; Reilly and Barlow, 1986), these parameters have been correlated with changes in population abundance for other marine mammal species (Fowler, 1987). For instance, a decrease in ASM was correlated with a decline in population abundance for baleen whale stocks (Lockyer, 1984). Similarly, a decrease in ASM for crabeater seals was correlated with an increase in the per capita availability of food resources resulting from the exploitation and subsequent reduction in size of baleen whale stocks (Bengtson and Laws, 1985). Likewise, ASM for the striped dolphin of the western Pacific declined in response to exploitation and reduced population abundance (Kasuya, 1985). Based on the predictions of population responses to changes in density (i.e., increases in ASM and decreases in pregnancy rates as population abundance increases) presented by Eberhardt (1977) and Eberhardt and Siniff (1977), we predicted a decline in the ASM for both the northern offshore and southern offshore stocks of spotted dolphin after 1974 as well as a lower ASM for the more heavily exploited northern offshore stock. Similarly, a higher fraction of sexually mature females pregnant and those simultaneously pregnant and lactating should be observed for the northern offshore stock.

## Methods

Since 1968, when the National Marine Fisheries Service (NMFS) first placed observers aboard U.S. vessels to observe fishery activities, life history data has been collected from all cetacean species incidentally killed in the ETP yellowfin tuna purse-seine fishery. Beginning in 1974, life history data collection procedures were standardized, and the original sampling scheme that selectively collected large, female specimens was replaced by a random sampling scheme that selected the first available dead dolphins brought aboard (Perrin and Oliver, 1982). In 1979, the Inter-American Tropical Tuna Commission (IATTC) joined the NMFS in placing observers aboard U.S. vessels and collecting life history data.

The offshore stocks of spotted dolphin are distinguished geographically as being north or south of 1° south latitude (Perrin et al., 1985). The specimens used in our study were collected from these areas, but the sample of northern offshore stock animals was additionally restricted to those animals collected west of 120° west latitude (Fig. 1). The northern offshore stock was sub-sampled because exploitation has not been spatially uniform. The yellowfin tuna purse-seine fishery began primarily as a coastal fishery in 1959 and gradually expanded farther offshore. The Commission's Yellowfin tuna Regulatory Area (CYRA) was established in 1968 by the IATTC and provides a useful boundary that separates the inshore fishery area from the westernmost region of the ETP yellowfin tuna fishery (Peterson and Bayliff, 1985). The area west of the CYRA was not fished until the late 1960's, and then only for a few months a year. Exploitation in this region has been significantly less than inside the CYRA but much more than in the southern area which has been fished only sporadically since the early 1970's (Punsly, 1983). Although spotted dolphin move along the 10°N latitude as well as from the south to the west (Perrin et al., 1979a; Au and Perryman, 1985; Reilly, 1990), owing to the large size of the area, interchange between areas is probably limited. A standardized data collection scheme was established at about the same time as the fishery expanded into the western and southern regions of the ETP, and therefore we anticipated that these two distinct geographic regions would provide the best opportunity for testing potential biological indices.

Female spotted dolphins with complete life history data (i.e., geographic position, total body length, teeth collected, and both ovaries examined) collected between 1974 and 1988 were selected for this study. Few specimens have been collected from the southern offshore stock, and therefore all available specimens were prepared. Specimens from the northern offshore stock were selected randomly by year and the sample sizes distributed as evenly as possible between years so that annual estimates of ASM could be calculated. A maximum of 50 specimens per year was the target for selecting specimens from the northern offshore stock sample because Hohn (1989) showed that a sample size of 50 accurately estimated ASM and reduced the variance from an estimate based on a sample size of 25. Thin sections of the teeth were prepared and aged by one of us (ACM) with techniques described in Myrick et al. (1983). Prior to estimating age, all specimens were numerically coded in random order to disguise the specimen number so that no inference could be made about the stock or collection year for any speci-

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[1] Smith, T. D. (ed.). 1979. Report of the status of porpoise stocks workshop (August 27–31, 1979, La Jolla, California). U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-79-41, 120 p.

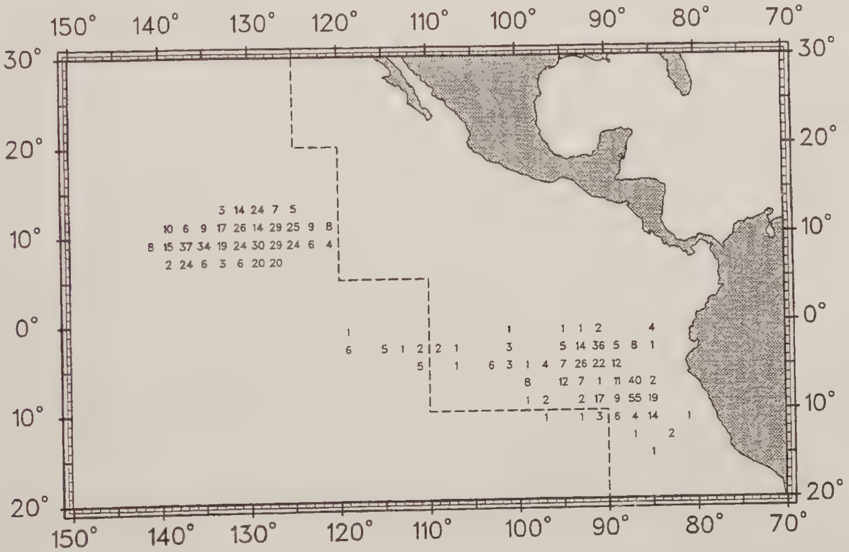

**Figure 1**

The collection location and sample size of female spotted dolphin specimens selected for this study summarized by 2°-degree square block. The sample of northern offshore spotted dolphins was selected from north of 1° south and west of the Commission's Yellowfin tuna Regulatory Area (the dashed line), and the sample of southern offshore spotted dolphins was selected from south 1° south.

men. The associated life history data were also withheld until each specimen was aged.

ASM and its variance were calculated with the following formula (DeMaster, 1984b; Hohn, 1989).

$$\mathrm{ASM} = x + \sum_{i=x}^{j} p_i$$

$$s^2 = \sum_{i=x}^{j} \{[(p_i * (1-p_i)]/(n_i-1)\},$$

where, $x$ = age of the youngest mature animal,
$j$ = age class of the oldest immature animal,
$p_i$ = proportion immature in age class $i$,
$n_i$ = sample size for age class $i$.

Because population abundance estimates are not available for the geographic areas from which our samples were collected, we substituted year as a correlate for evaluating potential biological indices. We tested for temporal trends in ASM with a linear regression to determine whether the slope was statistically significantly different from zero. In addition, data for each stock were pooled for all years, and the null hypothesis of no difference between estimates of ASM for the two stocks was tested with a Student's *t*-test.

Other reproductive parameters examined include the fraction of the females mature, and the fraction of mature females that were either pregnant or lactating, or simultaneously pregnant and lactating. Trends in these parameters between 1974 and 1988 were tested by using a chi-square test for linear trends (Snedecor and Cochran, 1973), and the mean estimates for each parameter, all years combined, were tested for statistically significant differences with a chi-square test.

## Results

### Average age at attainment of sexual maturity

ASM was estimated for each year with sufficient data available (Table 1): 1976–1982 and 1984–1988 for the northern offshore stock sample, and 1976, 1979, and 1982 for the southern offshore stock sample. The regression line fit to the data for the northern offshore stock was not statistically significantly different from zero. We did not fit a regression line to the data from the southern offshore stock because only three annual estimates were available. The pooled estimate of ASM for each stock was 11.1 years (SE=0.236; $n$=520) for

**Table 1**

Number of samples by year and state of sexual maturity (immature or mature) for the northern offshore and southern offshore stocks of spotted dolphin used to estimate the average age at attainment of sexual maturity.

| | Offshore stock | | | |
|---|---|---|---|---|
| | Northern | | Southern | |
| Year | Immature | Mature | Immature | Mature |
| 74 | 0 | 0 | 0 | 0 |
| 75 | 0 | 0 | 0 | 5 |
| 76 | 13 | 33 | 41 | 101 |
| 77 | 16 | 28 | 2 | 6 |
| 78 | 17 | 27 | 1 | 23 |
| 79 | 18 | 25 | 16 | 49 |
| 80 | 15 | 28 | 2 | 9 |
| 81 | 13 | 24 | 6 | 5 |
| 82 | 12 | 20 | 42 | 68 |
| 83 | 9 | 9 | 11 | 11 |
| 84 | 11 | 27 | 1 | 4 |
| 85 | 17 | 29 | 0 | 0 |
| 86 | 18 | 28 | 0 | 0 |
| 87 | 22 | 26 | 0 | 0 |
| 88 | 14 | 21 | 0 | 0 |
| Total | 195 | 325 | 122 | 281 |

the northern offshore spotted dolphin and 9.8 years (SE=0.264; $n$=403) for the southern offshore spotted dolphin (Fig. 2). This difference in the ASM was statistically significant ($t$=14.32, df=13, $P<$ 0.001). The range in age of animals attaining sexual maturity was largest for the northern offshore stock. The youngest mature animal was 7 years, and the oldest immature was 16 years. The same range for the southern offshore stock was 6 to 11 years (Fig. 3).

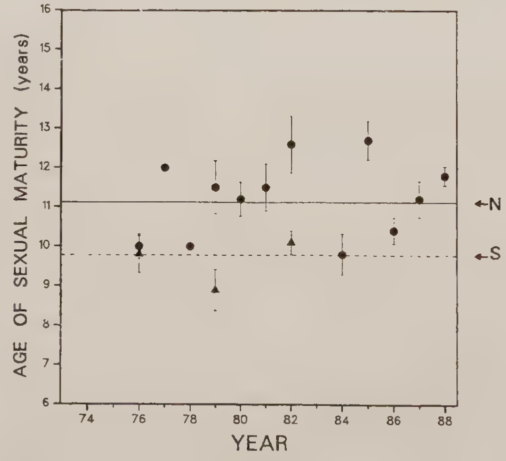

**Figure 2**

Estimates of the average age at attainment of sexual maturity (ASM) by stock for the offshore spotted dolphin with 1 SE. If no SE bar was plotted, then there were no overlapping indeterminate age classes. Circles represent estimates of ASM for the northern offshore stock and triangles are the estimates for the southern offshore stock. The pooled estimate of ASM for the northern offshore stock (N) is 11.1 years (solid line) and 9.8 years (dashed line) for the southern offshore stock (S).

## Reproductive rates

The statistically significant trends in the reproductive parameters examined were an increase in the proportion of mature females simultaneously pregnant and lactating in the northern offshore stock, the predicted compensatory response, and a decrease in the proportion of mature specimens in the sample from the southern offshore stock. When the data for all years were pooled, no statistically significant differences between the mean parameter estimates for the northern offshore and southern offshore stocks were detected (Table 2).

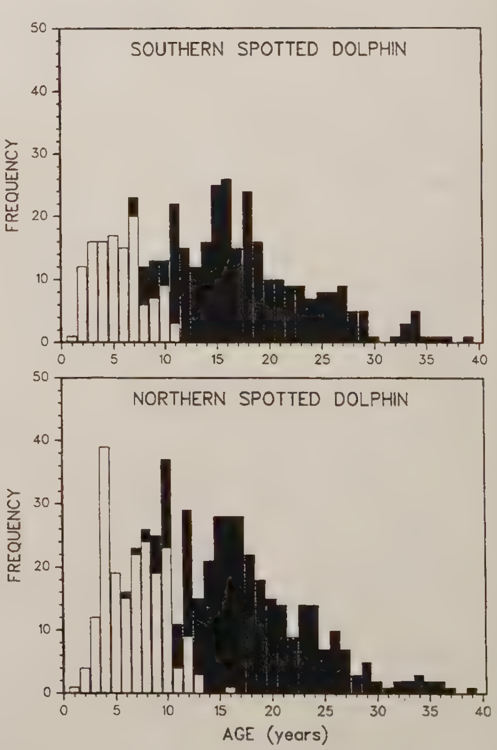

**Figure 3**

Age-frequency distribution of the northern offshore and southern offshore spotted dolphin specimens aged. The open bars represent the sexually immature females in the sample, and the solid bars represent the sexually mature females in the sample.

**Table 2**

The mean proportion of females by reproductive condition for the northern offshore and southern offshore stocks of spotted dolphin: the proportion of females in the sample that were sexually mature, and the proportion of sexually mature females that were pregnant or lactating, or simultaneously pregnant and lactating.

| Reproductive condition | Stock | |
|---|---|---|
| | northern | southern |
| Mature | 0.62 | 0.69 |
| Pregnant | 0.33 | 0.40 |
| Lactating | 0.55 | 0.47 |
| Pregnant and lactating | 0.06 | 0.06 |

## Discussion

Published evidence of density dependence in dolphin species is rare, and results are inconsistent. For example, in Japan, the striped dolphin, *Stenella coeruleoalba*, is heavily exploited, and the length of the lactation period is reported to have declined (Kasuya and Miyazaki[2]). For exploited spotted dolphins in the western Pacific, a decline in the ASM from 10.1 years in the 1961–63 cohorts to 8.6 years in the 1964–66 cohorts was reported, although the regression coefficient was not statistically significant (Kasuya, 1985). The decline in ASM for female striped dolphin from 9.7 years for the 1956–58 cohorts to 7.4 years in the 1968–70 cohorts was statistically significant (Kasuya, 1985). On the otherhand, for the spinner dolphin (*S. longirostris*) in the ETP, the less exploited southern whitebelly stock has a shorter lactation period than the more heavily exploited eastern spinner dolphin, the opposite of what would be expected for a compensatory response. The annual pregnancy rate, however, is lowest for the southern whitebelly stock and highest for the more heavily exploited eastern stock, as expected for density compensation (Perrin and Henderson, 1984). Barlow (1985) also reported differences in the proportion of mature female spotted dolphins (*S. attenuata*) that were pregnant between the eastern and western Pacific. The lowest proportion of mature females pregnant was observed in the more heavily exploited population, again, contrary to predictions based on the reported exploitation rates and estimates of population abundance for the ETP spotted dolphin. Also, for ETP spotted dolphins, the proportion of lactating mature females significantly increased from 46% in 1973 to 69% in 1981 ($P<0.05$) presumably in response to exploitation; no other statistically significant trends in reproductive parameters were found (Myrick et al., 1986).

Comparisons with other studies are difficult because in most cases the degree of exploitation relative to $K$ has not been quantified, and techniques to estimate age and ASM vary. In our study, statistically significant temporal trends were not detected for ASM but were detected for some of the reproductive parameters. The increase in the proportion of mature females simultaneously pregnant and lactating for the northern offshore stock and the decrease in the proportion of mature females in the population for the southern stock both suggest that the populations are growing. The fact that we did not observe the predicted compensatory responses in ASM may be due to one or more factors, including 1) too few data, 2) parameter estimation or measurement error, 3) a time lag in the response, or 4) biological differences between the stocks. Too few data and environmental periodicity (e.g., El Niño) may increase the variability in annual estimates of parameters, and both factors would reduce the ability to detect differences in potential compensatory responses (Goodman, 1984). The order in which parameters respond to changes in population density is not known, but time lags in responses may be expected owing to the late age at which these animals reach sexually maturity and the multi-year breeding cycle characteristic of the spotted dolphin (Goodman, 1981).

Data for the southern offshore stock of spotted dolphin, in particular, were limited and precluded testing for trends in ASM or the selected reproductive parameters. Although we selected our sample size, a maximum of 50 specimens per year for the northern offshore stock, on the basis of earlier work describing the effect of sample size on the variance for estimates of ASM (Hohn, 1989), our results indicate that larger sample sizes would be required to reduce the variance of the estimates in order to detect small, but biologically significant, changes (e.g., a 1.5-year difference) in ASM. Sample sizes of fewer than 50 per estimate of ASM resulted in too few specimens in the indeterminate age classes (i.e., those age classes with both sexually immature and mature animals) to estimate ASM accurately.

Another concern when analyzing data collected from a kill is whether the age distribution is representative of the population. All immature age classes appear to be underrepresented in both stocks, especially age classes between 10 and 15 years of the northern offshore stock (Fig. 3). This phenomenon was noted in a previous aging study of ETP spotted dolphin but occurred about five age classes earlier than the one we observed (Barlow and Hohn, 1984). This difference may be a result of different readers estimating age, although a Kolmogorov-Smirnov test to compare the age-frequency distributions of sexually immature and sexually mature animals from the two studies concluded that the samples were likely drawn from the same population. The underrepresentation of the immature age classes may be a result of segregation in the population by age and sex, fairly typical in large mammal populations, and may affect the estimation of ASM. We investigated the effect of this underrepresentation by assuming a stable age distribution and by apportioning the animals in the indeterminate age classes by sexual maturity under different assumptions of sexual maturity for animals in those age classes, and then calculated ASM. On the basis of segregation by age and sex observed in other species of large mammals, we predicted that the most reasonable scenario for reconstructing the age distribution is that the "missing" animals would be sexually immature. If this indeed were the case, we have underestimated ASM. Under this and other scenarios we investigated, estimates of ASM were consistently over- or under-estimated for both stocks. Therefore, possible sampling biases were unlikely to be responsible for the observed differences in ASM between the northern offshore and southern offshore stocks of spotted dolphin.

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[2] Kasuya, T., and N. Miyazaki. 1975. The stock of *Stenella coeruleoalba* off the Pacific Coast of Japan. Pap. ACMRR/MM/SC-25 pres. at FAO Scientific Consultation of Marine Mammals, Bergen, February, 1976, 36 p.

The hypotheses we tested required that several implicit assumptions be made, including: 1) constant data collection biases, 2) minimal interchange of animals between areas, 3) consistent estimation of specimen age, 4) linear compensatory response with change in population abundance, 5) constant carrying capacity (*K*), and 6) equivalent initial life history parameters for the two stocks. The first three of the assumptions are believed to hold reasonably well. Barlow (1985) tested several of the same life history parameters we examined and found them to be relatively insensitive to a number of potential data collection biases; no major changes in the collection of life history data were made after 1974, thus supporting constant data collection bias as a reasonable assumption. Furthermore, the fishery operates in the same areas from year-to-year at approximately the same time of year. In fact, 60% of our sample from the northern offshore stock was collected between July and September, and a further 38% was collected between April and June; in the south, 57% of the sample was collected between January and March, and 27% was collected between October and December. This pattern of sample collection was consistent from year-to-year, and therefore would not affect the pooled or annual estimates of ASM or reproductive parameters. Geographic variability has been noted in earlier studies of spotted dolphin life history data (Hohn and Hammond, 1985; Barlow, 1985); thus selecting specimens from discrete areas as we did reduces the potential for geographic variability to obscure population compensatory responses. Similarly, estimating the age of all specimens at one time and in the blind ensured that age estimates were made as consistently as possible. Information about the validity of assumptions 4) and 5) is not currently available, but violations of the assumptions may provide explanations for our results. There is evidence for differences in the morphological and life history characteristics between the northern offshore and southern offshore stocks of spotted dolphin (see Perrin et al., 1976, 1979b, 1991[3]; Barlow, 1985; Hohn and Hammond, 1985; Myrick et al., 1986; Bright and Chivers[4]) that are likely correlated with the different oceanographic environments of the areas inhabited by these stocks (Au and Perryman, 1985; Reilly, 1990).

We did not find conclusive evidence for compensatory responses in these stocks of spotted dolphin as only one reproductive parameter for each stock showed a statistically significant trend. However, observed trends in both parameters suggest the populations are below *K* and declining. Our comparison of ASM's suggest further biological differences between the northern offshore and southern offshore stocks or populations. Currently, the order of compensatory responses and their dynamics are not known. In order to be useful as a biological index, a measure of the status of the population must be known and the dynamics of the parameter over a wide range of population densities quantified (Fowler and Siniff, 1992).

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[3] Perrin, W. F., G. D. Schnell, D. J. Hough, J. W. Gilpatrick, and J. V. Kashiwada. 1991. Re-examination of geographical cranial variation in the pantropical spotted dolphin *(Stenella attenuata)* in the eastern Pacific. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-91-39, 46 p.

[4] Bright, A. M., and S. J. Chivers. 1991. Post-natal growth rates: a comparison of northern and southern stocks of the offshore spotted dolphin. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-91-30, 24 p.

Lockyer, Steve Reilly, and three anonymous reviewers whose comments on earlier drafts greatly improved the manuscript.

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# The Commercial, Subsistence, and Recreational Fisheries of American Samoa

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*ABSTRACT—Domestic fisheries in American Samoa landed 587,000 lb of fish and invertebrates in 1991 worth $993,000. Most of the catch (78%) and value (80%) was taken by the shoreline subsistence fishery that occurs on the coral reefs surrounding the islands. Artisanal fisheries for offshore pelagic fishes (primarily skipjack tuna,* Katsuwonus pelamis*; and yellowfin tuna,* Thunnus albacares*) and bottomfishes (snappers, emperors, groupers) accounted for 16% and 3%, respectively, of the domestic catch. Recreational tournament catches for pelagic fishes represented the remainder (3%).*

*While sport fishing is becoming increasingly important, other domestic fisheries have declined in recent years. The shoreline subsistence fishery has dropped by about 25% over the past decade owing to socioeconomic factors and possibly overexploitation. Artisanal fisheries have also declined precipitously in recent years owing to hurricane-related damages, attrition of fishermen, and competition with imports. Artisanal fisheries show some potential for growth, but may be constrained by marketing issues, vessel capabilities, and limited stock sizes (for bottomfish) or local availability of high-value (pelagic) fishes.*

*In contrast to the small-scale domestic fisheries, American Samoa is also homeport to a distant-water fleet of large purse seiners and longliners that fish beyond the EEZ and deliver about 160,000–220,000 short tons of tuna per year to local canneries.*

## Introduction

Many tropical islands in the South Pacific Ocean are confronted by rapidly growing human populations, but have few economic resources that their residents can utilize. Fish resources, from traditional subsistence fishing in times past to today's more modern boat-based fisheries, have always been an important component of island economies (Doulman and Kearney, 1991). It is therefore of interest to examine the current use and potential development of such fisheries. An overview of recent trends in the small, but locally important, domestic fisheries in American Samoa is presented in this paper. This includes four fisheries: 1) a shoreline subsistence fishery, 2) an artisanal fishery for offshore pelagic fishes, 3) an artisanal fishery for offshore bottomfish, and 4) a recreational tournament fishery. For completeness and contrast, the much larger distant-water fleet of commercial vessels that deliver tuna to canneries in American Samoa is also briefly described.

## Study Area

American Samoa, the only U.S. Territory in the southern hemisphere, consists of 7 small islands in the central South Pacific Ocean (Fig. 1). The largest islands are Tutuila and the Manu'a group (Ofu, Olesega, and Ta'u Islands). The total land area is only 77 mi.$^2$ . Most of the islands have steep volcanic slopes with limited flat land suitable for human habitation or agriculture. The Territory's population (46,600 in 1990), located primarily on Tutuila Island, is growing rapidly (3.7% per year) and has a doubling time of only 19 years (EDPO, 1991). The two major employers are the tuna canneries and the local government, which employ 33% and 31% of the labor force, respectively. There is a heavy reliance on imports for food, fuel, and materials (EDPO, 1991). Canned tuna is the only significant export, which supplies about 25% of all canned tuna consumed in the United States.

## Data Collection System

The Department of Marine and Wildlife Resources (DMWR) in American Samoa provides fisheries information to the National Marine Fisheries Service (NMFS) through its Western Pacific Fisheries Information Network (WPACFIN) and to the Western Pacific Regional Fishery Management Council (WPRFMC). The Council is responsible for managing fisheries within the 200–mile Exclusive Economic Zones (EEZ) around American Samoa, Hawaii, Guam, the Commonwealth of the Northern Marianas, and other U.S. possessions in the Pacific.

The historical development of DMWR has been described by Itano (1991). DMWR (initially the Office of Marine Resources) was established in the 1960's to oversee fisheries development projects and conduct resource assessments. In 1972, the development of artisanal fisheries began in earnest as did DMWR's data collection efforts. With assistance from WPACFIN in the 1980's, the data collection program was significantly upgraded and expanded to provide better coverage and statistics for all local boat-based fisheries.

General procedures for DMWR data collectors are to sample the artisanal fisheries two weekdays and one weekend (or holiday) per week, as described in detail by Aitaoto et al. (1991). During sample days, a creel survey is conducted as boats dock at designated harbors between 0500 and 2100 h. The fishermen are interviewed and their catches examined. To produce annual

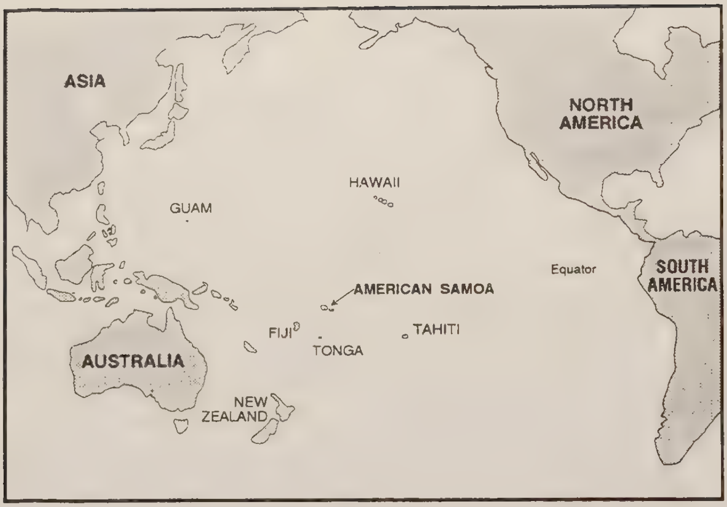

Figure 1.—Location of American Samoa (14° S, 170° W) in the South Pacific Ocean.

catch statistics, the creel survey information is computerized, verified, and expanded to account for times and areas not sampled. In the Manu'a Islands, the fishing fleet is small and the catch from nearly every boat is monitored; data are adjusted for the few trips not sampled. For recreational tournaments, DMWR provides the official weigh-in station and tallies landings from all participating boats.

The shoreline subsistence fishery on Tutuila Island was first examined in the late 1970's by Hill (1978) and Wass (1980). Beginning in 1991, the fishery is again being monitored by a creel and participation survey, conducted 3 days a week, stratified by time of day and type of day (weekday/weekend) (Ponwith, 1992). Catch data were first expanded to the entire study area along the south shore of Tutuila, where 35% of the people live. Then, on a per-capita basis, results were expanded to produce a Territorial catch.

The distant-water fleet that delivers tuna to canneries in American Samoa has been monitored by NMFS, either directly or by contract to DMWR, since 1963. The NMFS port sampling program collects vessel logbooks, length-frequencies of tuna species, and cannery summaries of vessel landings by species and gear type. Sampling procedures are described by Honda et al.[1] and Ito and Yamasaki[2].

## Regulations and Enforcement

Few of WPRFMC's regulations have focused on American Samoa's EEZ, because no major commercial fishery operates there at present. A goal, however, will be to insure that local residents have opportunities to participate in future fisheries developments that do occur. Preferential rights for indigenous people are currently being researched, and a control date (1 Jan. 1991) was set for possible implementation of a limited entry program for longline fishing. Occasional poaching by foreign vessels occurs in the EEZ, but no enforcement vessels or aircraft are available for surveillance.

Territorial regulations that apply to the management of local fisheries include record keeping for commercial fishermen, seafood dealers, and fish processors, as well as specific laws (mostly pertaining to reef users) regarding illegal fishing methods, gear restrictions, and species size limits. Enforcement of territorial regulations is at an early stage of development.

## Domestic Fisheries

The annual harvest of combined domestic fisheries in 1991 was 587,000 pounds, valued at $993,000 at local market prices. By far the majority of this catch (78%) and value (80%) was taken by the shoreline subsistence fishery (Fig. 2). It should be noted, however, that none of the domestic fisheries is strictly a commercial, subsistence, or recreational enterprise. These terms are used only to describe the principal nature of the fishery because some fish are sold and others are retained for personal use in each fishery. The percentage of fish sold varies consider-

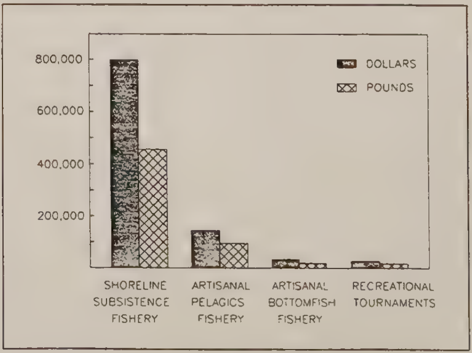

Figure 2.—Annual landings and value of four domestic fisheries in American Samoa in 1991. Units on the vertical axis refer to both dollars and pounds.

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[1] Honda, V., G. Yamasaki, and R. Ito. 1988. American Samoa purse seine fishery sampling. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Center., Honolulu Lab., Admin. Rep. H-88-20, 35 p.

[2] Ito, R., and G. Yamasaki. 1988. Status of the American Samoa foreign longline tuna fishery, 1982–86. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Admin. Rep. H-88–19, 30 p.

ably: Recreational tournaments (10% sold), shoreline subsistence fishery (25%), artisanal bottomfish fishery (65%), artisanal pelagic fishery (85%).

### Shoreline Subsistence Fishery

The islands of American Samoa are partially surrounded by a narrow fringing coral reef, the top of which is exposed at low tide. The reeftop and adjacent shallow waters are inhabited by a diverse array of fish and shellfish species (Wass, 1984; USACE[3, 4]) that are harvested by local residents on almost a daily basis throughout the year (Hill, 1978; Wass, 1980; Ponwith, 1992). Most fishing is accomplished by individuals on foot who fish in areas adjacent to their own village. Principal fishing methods used are rod and reel (which accounted for 37% of the annual catch in 1991), handline (25%), free diving (14%), gill netting (9%), gleaning (8%), and throw netting (5%). Gleaning involves the collection of fish and invertebrates at low tide, usually by hand, stick, or steel rod.

The 1991 island-wide subsistence catch on Tutuila Island was 439,000 pounds and was worth $768,000 at the average rate of $1.75/pound (Ponwith, 1992). Expanding these data to include limited catches in the Manu'a islands produces a total subsistence catch in the Territory of 456,000 lb, worth $798,000. The average catch per unit of effort (CPUE) was 3 pounds/gear-h; highest CPUE was obtained by gill netting (12.2 pounds/gear-h), followed by throw net (4.9 pounds/gear-h), free diving (2.9), rod and reel (2.9), gleaning (1.7), handline (1.4), and bamboo pole hook and line (0.7).

Virtually all fish and invertebrate species caught were retained for consumption or sale. Altogether, 69 species or species groups were harvested; fishes accounted for 86% of the total catch by weight. One coastal migratory fish species, the atule or bigeye scad, *Selar crumenophthalmus*, dominated the harvest in 1991 (Table 1). Jacks, surgeonfish, mullet, and octopus made up the majority of the reef-resident species taken. The average sizes of fishes taken were surprisingly small (Table 1), particularly for groupers and snappers which had very low mean weights (0.3–0.4 pound). Some favored species, such as giant clams, *Tridacna* spp., were generally absent in reef catches because of overharvesting.

Table 1.—Catch composition of the shoreline subsistence fishery on Tutuila Island in 1991.

| Reef species group | | Catch Composition (%) | Average Weight (lb) |
|---|---|---|---|
| Coastal Migrants | | | |
| Atule (big-eye scad) | *Selar crumenophthalmus* | 46 | 0.3 |
| Reef Residents | | | |
| Jacks | Carangidae | 10 | 1.4 |
| Surgeonfish | Acanthuridae | 9 | 0.5 |
| Mullet | Mugilidae | 6 | 0.9 |
| Octopus | *Octopus* sp. | 5 | 2.2 |
| Groupers | Serranidae | 3 | 0.4 |
| Sea urchins | Echinoid | 3 | |
| Palolo worms | *Eunice viridis* | 2 | |
| Squirrelfish | Holocentridae | 2 | |
| Snappers | *Lutjanus* spp. | 1 | 0.3 |
| Parrotfish | Scaridae | 1 | |
| Sea snails | Gastropoda | 1 | |
| Other | | 11 | |

Total catch: 439,000 pounds

One unique species taken was the palolo worm *Eunice viridis*, a burrowing polychaete. Palolo generally emerge once a year to release their reproductive segments (epitokes) into nearshore waters (Caspers, 1984; Itano and Buckley, 1988). Samoans, who consider the epitokes a delicacy, gather in large numbers (up to 1,000's) at midnight of the predicted night of emergence to collect the epitokes using scoop nets or long lengths of screen. Ponwith (1992) reported that palolo catches were highly variable (3,400 pounds in 1990, 600 pounds in 1991) because of the strength of the swarming event and the presence of offshore winds that concentrate the epitokes near the shoreline, making them more accessible to the villagers.

An opportunity to identify trends in the shoreline fishery was provided by two similar studies conducted in 1979 (Wass, 1980) and 1991 (Ponwith, 1992) on Tutuila Island. During this 12–year period, the island-wide catch decreased by 26%; however, differences in the run strength of the atule, an annually variable migrant to the shoreline area, tend to obscure an even greater decline in catch. In 1979 the atule catch was relatively small, only 13% of the total catch compared to 46% in 1991. By removing this species from the analyses and considering only the reef-resident species, a major drop is apparent in the adjusted island-wide catch (–54%) over the past 12 years, while effort decreased only 8% (Fig. 3).

Downward trends in catch and effort seem even more significant since there was a 46% increase in the human population during the same period (EDPO, 1991). With this influx of people and reduced fishing effort, the per capita subsistence catch on Tutuila Island dropped from 19.4 to 9.8 pounds. Some possible explanations for the reduced catch and effort include a decline in resource abundance (reflected by a drop in CPUE) or sociological changes such as less leisure time, a shift in dietary preferences, or a preference to buy fish at the market rather than to catch them personally. Imports of reef fish from Western Samoa and Tonga have occurred in recent years (at least 10,200 pounds in 1991) and appear to be increasing.

In general, the shoreline subsistence fishery appears to be declining, although it still far exceeds harvests of other domestic fisheries in American Samoa. Two notable exceptions to this apparent decline in interest are the directed fishing efforts for two highly prized species, the atule and palolo.

### Artisanal Fisheries

While local fishermen in American Samoa have harvested inshore fishes over the millennia, they have also made significant catches of offshore fishes since the 1970's. Itano (1991) describes in detail several "boom and bust" cycles that occurred over the years as various fisheries development projects were introduced. One of the more lasting projects was the small-boat "Dory Project" (1972–75) in which subsidized dory-type boats were made available to fishermen who then supplied catch information to DMWR. Though the project faded because of a variety of problems, Itano (1991) notes that it

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[3] USACE. 1980. Coral reef inventory of American Samoa. U.S. Army Corps Eng., Honolulu, Hawaii, 314 p.

[4] USACE. 1994. Coral reef inventory of American Samoa. U.S. Army Corps Eng., Honolulu, Hawaii.

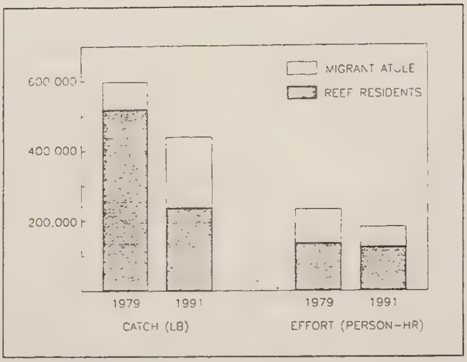

Figure 3.—Comparison of catch and effort in the shoreline subsistence fishery on Tutuila Island in 1979 (Wass, 1980) and 1991 (Ponwith, 1992).

inaugurated the current artisanal fisheries in American Samoa. Although catch statistics from the Dory Project are incomplete, CPUE data are available for comparison to current catch rates.

The two components of the current offshore artisanal fishery are 1) trolling for pelagic fishes in surface waters and 2) vertical handlines (with baited hooks) for bottomfish (Aitaoto et al., 1991). Fishing is typically conducted from small boats (e.g., 28-foot aluminum catamarans) fishing 1–25 miles offshore on 1-day trips. In 1991, boats participating in the pelagic fishery (30 boats) and bottomfish fishery (20 boats) landed relatively small amounts of fish, thus indicating the part-time nature of their participation in the fisheries. The average catch was about 130 pounds per trip in both fisheries, and the annual catch per vessel averaged 910 pounds of bottomfish and 3,030 pounds of pelagic fish.

### Artisanal Pelagic Fishery

Most pelagic fishing occurs in coastal waters, near seamounts, where seabird flocks are feeding (thus indicating the presence of baitfish that tuna may also be feeding upon), or at fish aggregation devices (FAD's) deployed around Tutuila Island. FAD's were introduced to American Samoan coastal waters in 1979 and have proven to be a popular way to increase the CPUE of widely dispersed pelagic fishes (Buckley et al., 1989). The lifespan of FAD's ranges about 3–30 months, and in recent years, 1–5 FAD's have been on station at any given time.

The artisanal catch of pelagic fish totaled 94,900 pounds in 1991, worth about $144,200 (this includes the value of pelagic fish retained for personal use) at an average price of $1.52/pound. Catches have ranged from 100,000 to 240,000 pounds in recent years (Fig. 4), and consisted primarily of skipjack and yellowfin tuna (Table 2). CPUE was variable (Fig. 5), as might be expected for oceanic migratory species, but current CPUE's are generally similar to CPUE's obtained during the start-up of the fishery in the 1970's (i.e., the Dory Project).

The recent drop in pelagic landings reflects, in part, recent hurricane-related damage (Hurricanes Tusi in 1987, Ofa in 1990, and Val in 1991), and the departure of several "highliners" from the fishery. Declines in revenue generated by the pelagic fishery (Fig. 6) from 1988 to 1990 were a result of drops in both landings and price; however, revenue made a slight comeback in 1991 owing to an increase in price. The pelagic fishery competes with an inexpensive and readily available supply of frozen fish that is purchased or bartered from foreign longline vessels delivering tuna to the canneries in American Samoa. In some cases, the domestic skippers themselves act as middlemen in such transactions. It is difficult to assess the influence that this fish source has on the market supplied by local fishermen, though Itano (1991) speculates that it inhibits the development of a viable artisanal fishery in the Territory.

**Table 2.—Catch composition of the artisanal pelagic fishery, 1989–91.**

| Pelagic species | | Catch in 1989–91 (%) Mean | Range |
|---|---|---|---|
| Skipjack tuna | *Katsuwonus pelamis* | 55 | 48–60 |
| Yellowfin tuna | *Thunnus albacares* | 28 | 26–32 |
| Blue marlin | *Makaira mazara* | 6 | 4–8 |
| Sharks | Miscellaneous | 3 | 2–4 |
| Dolphinfish | *Coryphaena hippurus* | 2 | 2–3 |
| Barracudas | *Sphyraena* spp. | 2 | 1–2 |
| Little tuna | *Euthynnus affinis* | 1 | 0–3 |
| Wahoo | *Acanthocybium solandri* | 1 | 1 |
| Dogtooth tuna | *Gymnosarda unicolor* | 1 | 1–2 |
| Other | | 1 | 0.2–1 |

Mean annual catch (lb): 124,200
Range (lb): 83,500–198,200

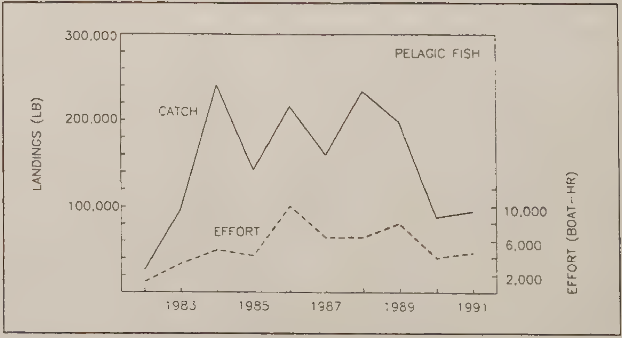

Figure 4.—Annual landings and effort of the artisanal fishery for offshore pelagic fishes.

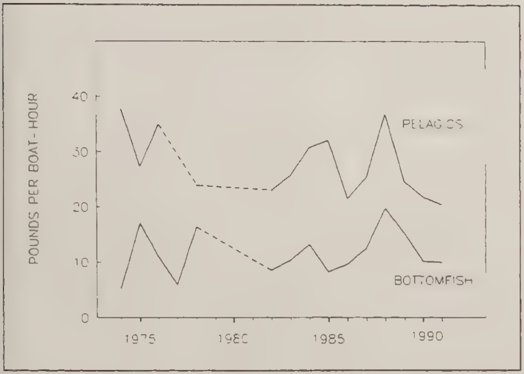

Figure 5.—CPUE trends for artisanal fisheries for bottomfish and troll-caught pelagic fishes. Data in 1977 were insufficient for pelagic catches, and no data were recorded in 1979–81.

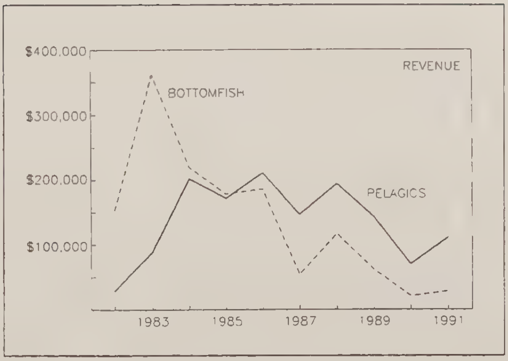

Figure 6.—Annual revenue (inflation adjusted) for artisanal fisheries for bottomfish and pelagic fishes. This graph illustrates commercial sales but does not include the value of fish retained for personal use.

## Artisanal Bottomfish Fishery

Bottomfish fishing occurs at depths of 15–100 fm around Tutuila Island and offshore seamounts. Suitable habitat for bottomfish is limited because the islands slope steeply into deep water and there are few seamounts in the Territory. The 100–fm isobath extends 110 n.mi. around the seven islands of American Samoa and 34 n.mi. around its seamounts (Itano, 1991). Dalzell and Preston (1992) estimate that the maximum sustainable yield (MSY) for deep slope bottomfish is about 8–27 t/year.

A small fishery for bottomfish was developed as a result of several government-funded projects in the 1970's and 1980's, and some high-valued fish (e.g., deepwater snappers) were shipped to Hawaiian markets for higher prices. But as these projects terminated and catches dropped, interest waned, and the fishery declined. The fishing grounds were "fished out" and catches probably exceeded MSY during this period (Itano, 1991).

In the past several years, the bottomfish fishery has collapsed to only 14% of its 1985 peak year (Fig. 7), and no fish are being marketed off the island. This decline appears to be due to several factors in addition to overfishing: Decreased subsidies to the fishery (Itano, 1991), the departure of several highliners from the fishery, and hurricane-related damage to local boats.

Snappers, emperors, and groupers accounted for most of the 18,100 pounds of bottomfish landed in 1991 (Table 3). This catch was worth $32,800 (this includes the value of bottomfish retained for personal use) at an average price of $1.81/pound. CPUE has varied between 10 and 20 pounds/boat-h, which is similar to CPUE's from the Dory Project in the 1970's (Fig. 5).

Revenue trends for the bottomfish fishery parallel the decline in catch (Fig. 6). Fishermen are also beginning to experience marketing conflicts with the recent influx of fresh bottomfish imported from Western Samoa and Tonga. In 1991 (the first year for which nearly complete data are available), imports of bottomfish were at least 19,400 pounds, thereby exceeding local landings of bottomfish.

## Tournament Fishery

Tournaments for pelagic fishes are popular events in the Territory. Typically, 7–14 local boats and 55–70 fishermen participate in each tournament, which are held 2–5 times per year, each lasting about 3 days. Tournament landings have been monitored almost yearly since 1974.

During 1974–92, the average fishing trip lasted 10 h and caught 12.3 pounds fish, for a daily trip average of 118 pounds (range 0–949 pounds), all species combined. After cancellation

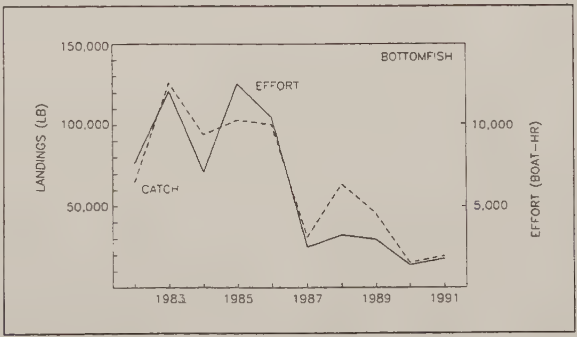

Figure 7.—Annual landings and effort of the artisanal fishery for bottomfish.

of most tournaments in 1990 in the aftermath of Hurricane Ofa, a sharp increase in participation and catches (as well as monitoring efforts) occurred in 1991 (Fig. 8). All reported landings (Fig. 8) are considered minimum estimates because 1) skipjack tuna and sharks were caught but often not reported because there was no tournament prize for them and 2) a fish caught might not be reported if a larger prize-winning one had already been landed.

The species composition of the five tournaments in 1991 consisted primarily of yellowfin tuna, blue marlin, and skipjack tuna (Table 4). Average and maximum weights of fishes caught (Table 4) are smaller than Hawaiian records, perhaps due to a much lower sport fishing effort in American Samoa.

**Table 3.—Catch composition of the artisanal bottomfish fishery, 1989–91.**

| Bottomfish species | | Catch in 1989–91 (%) Mean | Range |
|---|---|---|---|
| Bluelined snapper | *Lutjanus kasmira* | 17 | 14–20 |
| Redgill emperor | *Lethrinus rubrioperc.* | 12 | 11–14 |
| Gray jobfish | *Aprion virescens* | 10 | 7–14 |
| Longnose emperor | *Lethrinus elongatus* | 7 | 4–10 |
| Lunartail grouper | *Variola louti* | 6 | 5–8 |
| Other groupers | Serranidae | 6 | 2–10 |
| Humpback snapper | *Lutjanus gibbus* | 5 | 4–6 |
| Ambon emperor | *Lethrinus amboinensis* | 4 | 3–5 |
| Squirrel. snapper (ehu) | *Etelis carbunculus* | 4 | 3–6 |
| Jacks (unidentified) | *Carangidae* | 4 | 3–6 |
| Black jack | *Caranx lugubris* | 3 | 3–4 |
| Twinspot/red snapper | *Lutjanus bohar* | 3 | 2–4 |
| Longtail snapper (onaga) | *Etelis coruscans* | 3 | 2–4 |
| Other emperors | *Lethrinidae* | 3 | 2–4 |
| Peacock grouper | *Cephalopholis sonnerati* | 2 | 2–3 |
| Silverjaw jobfish (lehi) | *Aphareus rutilans* | 2 | 1–3 |
| Opakapaka | *Pristipomoides* spp. | 2 | 1–3 |
| Kusakar's snapper | *Paracaesio kusakarii* | 2 | 0–5 |
| Flower snapper (gindai) | *Pristipomoides zonatus* | 1 | 1–2 |
| Other | | 3 | 1–5 |

Mean annual catch (lb): 26,300
Range (lb): 15,400–45,300

**Table 4.—Catch composition and weight of fish caught in recreational fishing tournaments. Note that record weights for sharks and skipjack tuna may be artificially low because these were not target species.**

| Species | Composition in 1991 (%) | Tournament records[1] (lb) Mean | Maximum |
|---|---|---|---|
| Yellowfin tuna | 36 | 16 | 185 |
| Blue marlin | 23 | 132 | 542 (636)[3] |
| Skipjack tuna | 19[2] | 9 | 36 |
| Wahoo | 8 | 19 | 54 |
| Mahimahi | 6 | 23 | 51 |
| Sailfish | 4 | 75 | 110 |
| Shark | 1[2] | 87 | 125 |

[1] 1974–1992

[2] Minimum estimate due to incomplete reporting

[3] A nontournament blue marlin weighing 636 pounds was caught in 1984, and a larger one was caught but not recorded (H. Sesepasara, personal commun.).

The tournament CPUE for targeted species (blue marlin, yellowfin tuna, wahoo, and mahimahi) has been increasing over the years (Fig. 8), probably for several reasons. The fishermen are using better fishing gear and they have larger boats that can go farther offshore to fish around seamounts. In addition, the introduction of FAD's around Tutuila Island has resulted in higher catch rates (Buckley et al., 1989).

Tournament fishing is becoming increasingly important in American Samoa, and it contributed 3% of the total domestic landings in 1991 in only 16 days of fishing. The catch during this short period nearly equalled the yearly artisanal bottomfish harvest and amounted to 19% of the artisanal pelagic harvest.

## Commercial Tuna Fishery

In contrast to the small-scale nature of the domestic fisheries, American Samoa is also homeport to a distant-water fleet of large commercial vessels that deliver tuna to the canneries on Tutuila Island. These vessels fish beyond American Samoa's EEZ in the central and western Pacific Ocean. Fleet composition and landings have changed over the nearly 40 years that the canneries have been in operation, but it is beyond the scope of this paper to document these changes (see reports by Otsu and Sumida, 1968; Yoshida, 1975; Doulman, 1987; Schug and Galea'i, 1987; Honda et al.[1]; Ito and Yamasaki[2]).

The current fleet consists of 1) U.S. purse seiners that fish for skipjack and yellowfin tuna (about 30 vessels), 2) U.S. trollers that fish for albacore (about 30 vessels), and 3) foreign longliners that fish for albacore, yellowfin tuna, and bigeye tuna (about 70 vessels, mostly Taiwanese). In addition, transshipments of tuna are delivered to American Samoa by freezer vessels, and foreign sashimi longliners occasionally deliver part of their catch to the canneries.

Annual tuna landings in American Samoa have run about 160,000–220,000 short tons in recent years. Skipjack tuna accounted for most of the deliveries, followed by yellowfin tuna and albacore (Fig. 9). The catch by gear type was purse seine (50%), longline (14%), and troll (1%). The remainder (34%) was fish caught by purse seine and delivered to the canneries by freezer vessels.

## Discussion

Domestic fisheries may be small by commercial standards, but they are locally significant to the economy of American Samoa. The yearly harvest, originating primarily from the subsistence fishery on the coral reefs around

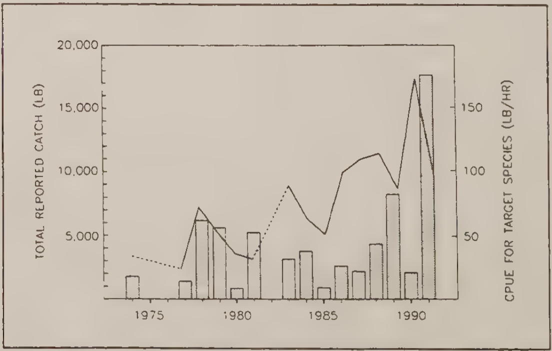

Figure 8.—Total reported catch of all species in fishing tournaments (bars) and CPUE (line) for the four principal target species: Blue marlin, yellowfin tuna, wahoo, and mahimahi. No data are available for 1975–76 and 1982.

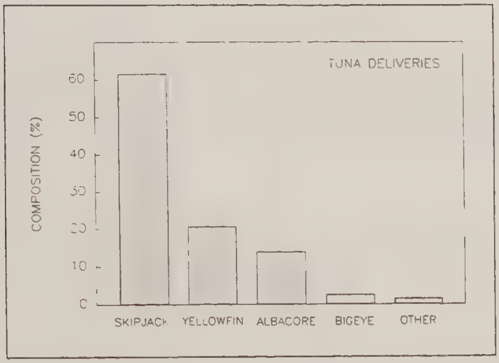

Figure 9.—Species composition of tuna delivered to canneries in American Samoa by the distant-water fleet of large commercial purse seiners and longliners.

the islands, amounted to 587,000 pounds worth nearly a million dollars in 1991. This dollar value does not fully represent the economic or social significance of this resource because of the subsistence component of Samoan culture and the generally low wage scale received by islanders who are employed.

A general decline in the catch and effort in the shoreline subsistence fishery has been noted, as might be expected in a society undergoing a shift from a subsistence economy to a cash economy. Nonetheless, the shoreline subsistence fishery still accounts for the major share of the total domestic catch and value. Consequently, there is a continuing need for the islands to better protect their reef resources from adverse impacts, some of which are readily apparent (e.g., pollution, siltation, destructive fishing practices). The scarcity of some highly sought reef species (e.g., giant clams), and the small sizes of fishes presently caught in the shoreline fishery also indicate that overfishing is probably occurring for some species.

Which of the domestic fisheries, if any, holds promise for further development? For the reasons outlined above, the shoreline subsistence fishery is an unlikely candidate. Similarly, the bottomfish fishery has already peaked because of the limited amount of suitable bottom habitat required by those species. However, considering the low level of fishing that occurs at present, the bottomfish fishery could withstand some increase in harvest.

Probably the least developed domestic fishery is that for pelagic fishes (tuna, marlin, swordfish, etc.) in the offshore waters of the Territory. These fishes are presumably part of large oceanic stocks which are unlikely to be diminished by small-scale artisanal fishing efforts. Rather, any expansion of this fishery will likely depend on several other factors. First, there are few local vessels at present that are large enough to undertake the multiple-day fishing trips necessary to fish profitably. None have freezer capabilities, and an adequate shoreside supply of ice is not yet available. Second, an increased supply of fish would quickly saturate local demands for fish, thus necessitating off-island marketing and shipping costs. Third, although pelagic resources are vast, their local availability may fluctuate because of seasonal variations or local depletions. Thus, a successful fishing enterprise by local residents would need to resolve important issues regarding vessel capabilities, marketing, and the availability of high-valued pelagic fishes in Territorial waters. However, an expansion of the sport fishery for pelagic fishes is not similarly encumbered, and indeed appears to be gaining popularity.

## Acknowledgments

The Department of Marine and Wildlife Resources appreciates the assistance provided by NMFS and WPACFIN in developing programs to monitor commercial fisheries within the Territory. The U.S. Fish and Wildlife Service provided funding through the Federal Aid in Sport Fish Restoration Act to examine noncommercial catches. We also thank Dave Itano and Dick Wass for their comments on this paper; Elliott Lutali for data processing; and Ioelu Seve, Alama Tua, Aitofele Sunia, Pita Ili, and Fa'apouli Niumata for data collection.

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# *Hapalotrema dorsopora* sp. n. (Trematoda: Spirorchidae) from the Heart of the Green Turtle (*Chelonia mydas*) with a Redescription of *Hapalotrema postorchis*

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ABSTRACT: *Hapalotrema dorsopora* sp. n. from the heart of the green turtle *Chelonia mydas* is described. *Hapalotrema dorsopora* differs from all other members of the genus by having a separate dorsal uterine pore. *Hapalotrema dorsopora* most resembles *Hapalotrema mehrai* Rao, 1976, but differs, in addition to separate dorsal and ventral pores, in placement of testes and vitellaria and shape of ovary. *Hapalotrema postorchis* Rao, 1976, originally described from a single specimen, is redescribed.

KEY WORDS: Trematoda, *Hapalotrema dorsopora* sp. n., Spirorchidae, green turtle, *Chelonia mydas*, Hawaii.

From 1986 to 1988, 10 green sea turtles (*Chelonia mydas* L.) were found stranded on the islands of Lanai, Maui, and Oahu in Hawaii. The turtles were covered with neoplasms identified as fibropapillomas. Upon determination that the turtles would not survive, they were killed and examined for parasites. Eight turtles, 6 from Oahu, 1 from Lanai, and 1 from Maui, were found infected with an undescribed species of the genus *Hapalotrema* Looss, 1899.

## Materials and Methods

Worms were placed in tapwater and refrigerated overnight, fixed in alcohol–formalin–acetic acid for 2 days, and then transferred to 70% ethyl alcohol for storage. Whole mounts were stained in Semichon's acetocarmine, dehydrated in a graded alcohol series, and mounted in Canada balsam. Specimens for scanning electron microscopy were critical-point dried using $CO_2$ as the transition fluid in a Polaron critical-point dryer and mounted on specimen stubs using conductive graphite paint (TV tube coat). Specimens were coated for 10 min at 10 mA with gold-palladium in a Technics Hummer V sputter coater and examined with an AMR 1000 at 8–20 kV. All measurements are in micrometers unless otherwise indicated and are given as a range with the mean in parentheses. Illustrations were made with the aid of a drawing tube. Voucher specimens have been deposited in the USNM Helminthological Collection.

## Results

Seven species of digenetic trematodes were collected from 10 specimens of green turtles in Hawaii (Table 1). Trematodes of the genus *Hapalotrema* occurred as 35% of total worms recovered and in 80% of turtles examined.

## Description

### *Hapalotrema dorsopora* sp. n.
(Figs. 1–3, 7)

*Hapalotrema dorsopora* sp. n. Spirorchidae Stunkard, 1921. The following description based on 10 specimens.

SPECIFIC DIAGNOSIS: Body elongate, 9.2–10.6 mm (9.9) long, maximum width 0.59–1.1 mm (0.86) at midbody. Oral sucker terminal, 420–450 (430) long by 360–370 (368) wide. Esophagus tubular, 630–720 (680) long surrounded by large gland cells at bifurcation (at 8% of body length) anterior to acetabulum. Intestinal ceca slightly sinuous, terminating posteriorly near anterior end of Y-shaped excretory vesicle. Acetabulum larger than oral sucker, discoid, covered with minute spines, pedunculate, with folded outer margin, 583–684 (610) in diameter. Peduncle 526–631 (578) long by 390–430 (410) wide. Testes numerous, 78–177 (119) long by 52–112 (78) wide, separated into pre- (47–56) and postovarian (48–54) groups filling intercecal space. External seminal vesicle 262–396 (308) long by 90–195 (139) wide, intercecal, transverse between preovarian testes group and ovary. Cirrus sac 270–338 (297) long by 60–90 (73) wide with internal seminal vesicle, ejaculatory duct and cirrus. Male genital pore median, ventral, and sinistral to ovary. Ovary oval, submedian, with irregular margins, 577–763 (665) long by 579–736 (666) wide, between testicular groups. Seminal receptacle immediately posterior to ovary. Dorsal uterine pore, median, on raised muscular pad (Fig. 7), 21 posterior to vitelline

**Table 1. Digenetic trematode parasites found infecting 10 green turtles from Hawaii.**

| | Locality* | USNM Coll. No. | Prevalence | Mean intensity | Range |
|---|---|---|---|---|---|
| *Learedius learedi* | 1, 3 | 82321 | 40% | 20.0 | 4–43 |
| *Hapalotrema dorsopora* | 1, 2, 3 | 82326 | 80% | 8.0 | 3–20 |
| *Polyangium linguatula* | 1, 2 | 82322 | 40% | 3.5 | 1–9 |
| *Angiodictyum longum* | 1, 2 | 82323 | 30% | 3.0 | 2–5 |
| *Hapalotrema postorchis* | 1 | 82324 | 30% | 6.0 | 2–14 |
| *Carettacola hawaiiensis* | 1, 3 | 81897 | 30% | 10.0 | 3–17 |
| *Pyelosoma cochlear* | 1 | 82327 | 10% | 19.0 | 19 |

* 1, Oahu; 2, Lanai; 3, Maui.

reservoir. Vitellaria mostly extracecal extending from pretesticular region to posterior extremity. Uterus short with metraterm, looping posteriorly from ovary to dorsal uterine pore. Eggs ($N = 10$) elongate with single or double polar filaments, 144–196 ([illegible]) long by 20–32 (26) wide.

HOST: Green turtle, *Chelonia mydas* L.

LOCATION: Heart.

LOCALITY: Kailua Bay, Oahu, Hawaii.

HOLOTYPE: USNM Helm. Coll. No. 82326.

PARATYPE: USNM Helm. Coll. No. 82327.

ETYMOLOGY: Dorso (L) = back; pora (L) = pore.

REMARKS: The new species most resembles *H. mehrai* Rao, 1976, but differs in size (*H. dorsopora* is larger); disposition of testes (first few preovarian testes only in 2 rows in *H. mehrai*, not found in *H. dorsopora*); placement of vitellaria (begin just posterior to acetabulum in *H. mehrai*, just anterior to testes in *H. dorsopora*); ovary entire in *H. mehrai*, irregular in *H. dorsopora*; dorsal uterine pore present in *H. dorsopora*, absent in *H. mehrai*.

### *Hapalotrema postorchis* Rao, 1976
### (Figs. 4–6)

Redescription based on 10 specimens. Body elongate, 10.3–12.8 mm (11.6) long, maximum width 1.0–1.8 mm (1.3). Tegument spinose; spines lost in frozen specimens. Oral sucker terminal, small, subspherical, 230–330 (250) wide by 240–360 (275) long; pharynx absent; esophagus narrow, thin-walled, 810–870 (832) long; bifurcating at 6–8% (7%) body length, just anterior to acetabulum, into 2 slender ceca, which extend to posterior extremities. Acetabulum slightly pedunculate, spherical, larger than oral sucker, 420–910 (714) in diameter, perimeter of sucker spinose, anterior edge at 9–12% (10.5%) body length. Testes few, 15–18 (17) measuring 430–620 (496) long by 280–420 (372) wide, separated by ovary into pre- (7–11) and postovarian (6–9) groups. Cirrus pouch large, 710–900 (840) long by 240–310 (285) wide, with internal seminal vesicle, ejaculatory duct and cirrus. External seminal vesicle transverse, between preovarian testes and ovary, measuring 480–670 (590) long by 250–380 (310) wide. Genital pore sinistral at lower level of ovary. Ovary lobed, between third and fourth quarter of body, 710–870 (775) long by 470–680 (618) wide. Vitellaria inter- and extracecal beginning 638–1020 (842), postacetabulum. Uterus short with metraterm. Eggs ($N = 10$) elongate with polar filament on each end measuring 140–330 (168) × 29–41 (32).

HOST: *Chelonia mydas* L.

LOCATION: Heart.

LOCALITY: Pamban, South India, Gulf of Manar (type locality; Rao, 1976). Kaneohe Bay, Oahu, Hawaii (this study).

VOUCHER SPECIMEN: USNM Helm. Coll. No. 82324.

REMARKS: According to the original descrip-

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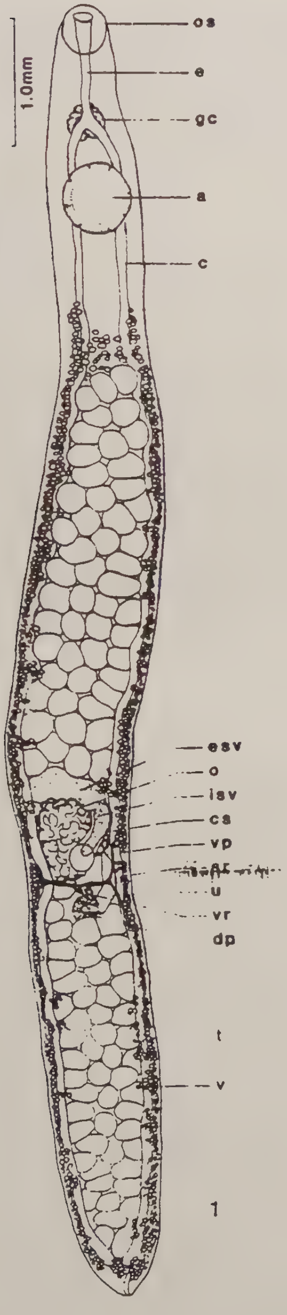
**Figures 1–6.** 1–3. *Hapalotrema dorsopora* sp. n. 1. Entire worm (ventral view). 2. Outline of entire worm (lateral view) showing pedunculate acetabulum, placement of dorsal and ventral openings; 3. Egg. 4–6. *Hapalotrema postorchis* redescription. 4. Entire worm (ventral view). 5. Outline of worm anterior showing slightly pedunculate acetabulum (lateral view). 6. Egg. a, acetabulum; c, cecum; cs, cirrus sac; dp, dorsal pore; e, esophagus; esv, external seminal vesicle; gc, gland cells; isv, internal seminal vesicle; o, ovary; os, oral sucker; sr, seminal receptacle; t, testis; u, uterus; v, vitellaria; vp, ventral pore; vr, vitelline reservoir.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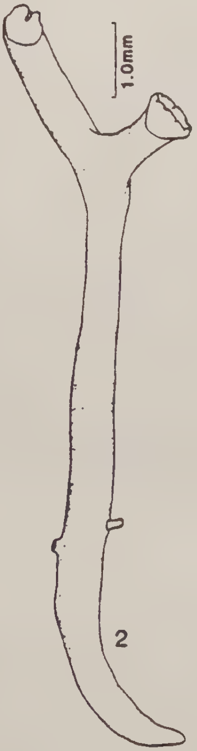
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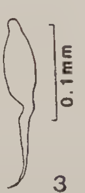
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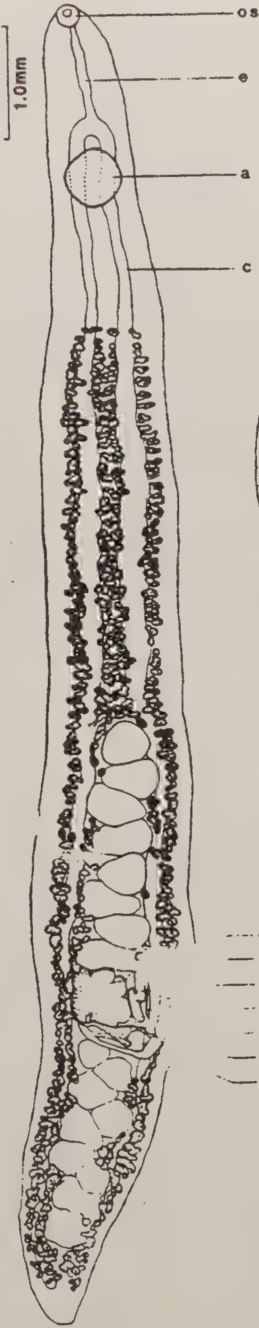
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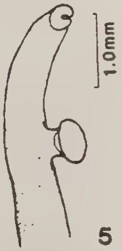
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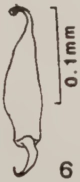
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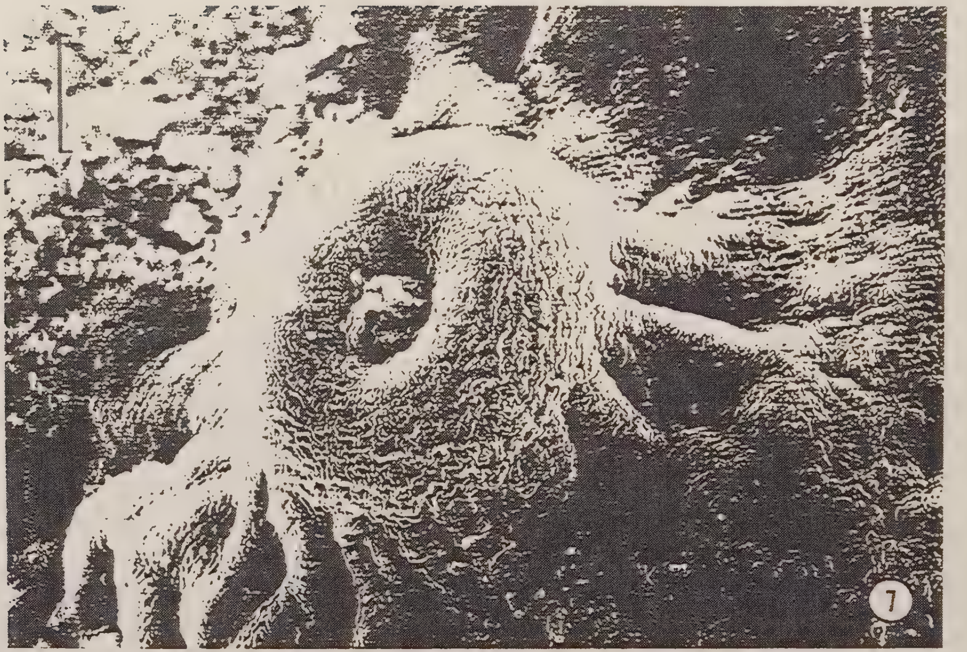

**Figure 7.** ***Hapalotrema dorsopora*** **sp. n. Scanning electron micrograph of dorsal uterine pore showing large, muscular-raised base. Scale bar = 30 μm.**

tion by Rao (1976), the measurements were taken from only 1 specimen. The specimen was not deposited in any collection and all attempts to examine the type material were unsuccessful. Differences seen between worms of this study and the Rao description are as follows. The acetabulum is slightly pedunculate and ringed with fine spines in the Hawaiian specimens. The total number of testes of the worm figured in the 1976 publication is shown at 19 (9 pre- and 10 postovarian). In our study, the maximum number found in any specimen examined was 18. The ceca are figured by Rao as bifurcating widely enough to circumvent the acetabulum. In the Hawaiian specimens, the ceca always continued behind the ventral sucker. Also, the vitellaria placement differs between the material in this study and those of the original description (beginning more posteriad in the Hawaiian material).

### Discussion

The blood flukes of sea turtles have been reviewed recently by Smith (1972) and Glazebrook et al. (1989). The genus *Hapalotrema* is separated from other members of the subfamily Hapalotrematinae Stunkard, 1921, by its large number of testes divided by the ovary and terminal genitalia into 2 groups (Yamaguti, 1958; Skrjabin, 1964). Smith (1972) lists 5 species of *Hapalotrema* in his review (*H. loossi* Price, 1934; *H. mistroides* (Monticelli, 1896) Stiles and Hassall, 1908; *H. orientalis* Takeuti, 1942; *H. polesianum* (Ejsmont, 1927) Byrd, 1939; *H. synorchis* Luhman, 1935). Glazebrook et al. (1989) list only 3 species of *Hapalotrema* in their table "Cardiovascular flukes recovered from sea turtles (1962 to present day)." There are currently 7 recognized species of *Hapalotrema* (Smith, 1972, omitted the 2 species from India, *H. mahrai* and *H. postorchis*, both described by Rao, 1976). All *Hapalotrema* species were described from marine turtles except *H. polesianum*. This species was originally found in the freshwater turtle *Emys orbicularis* and published as *Spirhapalum polesianum* by Ejsmont (1927) and later transferred to *Hapalotrema* by Byrd (1939). Only *H. mehrai* and *H. postorchis* have previously been recorded from *C. mydas*. *Hapalotrema loossi*, *H. synorchis*, and *H. mistroides* were all found in the loggerhead turtle (*Caretta caretta*) in Egypt, Florida, and an unknown locality, respectively. *Hapalotrema orientalis* was found in the hawksbill (*Eretmochelys squamosa*) on the island of Okinawa, Japan.

Two genera (*Hapalorhynchus* Stunkard, 1922, and *Coeuritrema* Mehra, 1933) from freshwater turtles have dorsal genital pores. However, the size of those pores is much smaller and less muscular than that described for *H. dorsopora*. This is the first report of a spirorchid trematode with separate dorsal (uterus) and ventral (cirrus) openings.

### Acknowledgments

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## New Book Available

NEMATODE PARASITES OF VERTEBRATES: THEIR DEVELOPMENT AND TRANSMISSION, by R. C. Anderson, 1992, C. A. B. International, 600 pp. (hardback) ISBN 0 85198 799 0. Available from The University of Arizona Press, 1230 North Park Avenue, Tucson, Arizona 85719. US$142.50 (Americas only).

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HERPETOLOGICAL JOURNAL, Vol. 3, pp. 81-83 (1993)

# A STRUVITE FAECOLITH IN THE LEATHERBACK TURTLE *DERMOCHELYS CORIACEA* VANDELLI: A MEANS OF PACKAGING GARBAGE?

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## ABSTRACT

A large stone-like object was collected from the rectum of a leatherback turtle beached at Midway Atoll, Hawaiian Islands. It consisted of biomineralized faecal material, the mineral being struvite ($NH_4MgPO_4.6H_2O$). Much material of anthropogenic origin (plastics in sheet and linear form, plus other packaging materials and monofilament nylon) was incorporated into the faecolith structure. It is hypothesized that the formation of struvite stems from the interaction of the leatherback's osmotic physiology with the metabolism of faecal bacteria. While the formation of the faecolith may be pathological, it could alternatively be an adaptive response to package garbage (whether natural or man-made).

## INTRODUCTION

Beached adult specimens of the leatherback turtle *Dermochelys coriacea* Vandelli have almost invariably been drowned in nets, injured/killed by shark attack or in collision with boats. They may therefore be presumed to have been healthy beforehand. Necropsy sometimes reveals hard, round objects in the gut, particularly the hind gut. For example, the large male leatherback beached at Harlech in North Wales, UK (Eckert & Luginbuhl, 1988) had a hard, clay-like ball at the junction between the small and large intestines, while the rectum of a turtle beached at Midway Atoll in the northwestern Hawaiian Islands contained a hard, smooth, ovoid ball (the subject of this article). The aim of this investigation was to analyze the nature of this object, and perhaps elucidate the reasons for the occurrence of such faecoliths.

## MATERIALS AND METHODS

A large (13 cm in diameter), smooth, stone-like object was collected (on 1.4.91) from the rectum (at the junction with the cloaca, but displaced to one side of the gut in an outpouching of the rectum) of a freshly-stranded specimen of *Dermochelys coriacea* at Midway Atoll at the northwestern end of the Hawaiian archipelago (28° 13' N, 177° 21' W) (see Fig. 1) . Leatherbacks are known to forage in the pelagic habitat to the north of Midway Atoll where they are not uncommonly entangled in Japanese, Taiwanese and Korean driftnets (Balazs, 1982). However, this was the first leatherback ever known to strand at Midway. The turtle had clearly been the victim of a shark attack as it had been decapitated very recently and lost all four flippers. Fresh blood was still flowing from its wounds and several sharks were swimming in shallow water immediately off the beach where the turtle stranded. On dissection (which revealed perfectly fresh tissues) the object was found immediately, so cannot have been an artifact of post-mortem deterioration.

The object was divided into two portions, one being sent to the UK for detailed analysis, while the other was used only for gross investigation. The faecolith portion sent to Britain was held for a few days in a water-saturated atmosphere. This caused the structure to soften. It was broken up and studied beneath a binocular microscope. During these observations, numerous small, hard, transparent crystals were seen embedded in the brown material of the softened faecolith structure. The crystals were dense and insoluble in water; they were separated from the rest of the material by washing and stirring. Crystals were prepared for X-ray probe microanalysis by freeze drying and attachment to an aluminium stub with double-sided adhesive tape. Crystals were studied in a scanning electron microscope (SEM) fitted with an energy dispersive X-ray microanalyser. A total of 10 faecolith crystals were investigated.

Once the elemental composition had been established, further crystals were investigated by X-ray diffraction. 20-30 of the larger and cleaner crystals were hand-picked under a binocular microscope and ground in an agate pestle and mortar under deionized water. The resultant slurry was spotted onto a glass slide and allowed to dry at room temperature. During drying the slurry was mixed using a scalpel blade in an attempt to minimize any preferred orientation. A diffractometer trace was obtained from this slide using CuK$\alpha$2 radiation in a Philips diffractometer.

## RESULTS

### GENERAL DESCRIPTION OF FAECOLITH

At the macroscopic level it was found that the smooth, rounded faecolith contained much material of anthropogenic origin (see Table 1). The rest of the faecolith appeared to be of an amorphous brown nature, with a strong faecal odour.

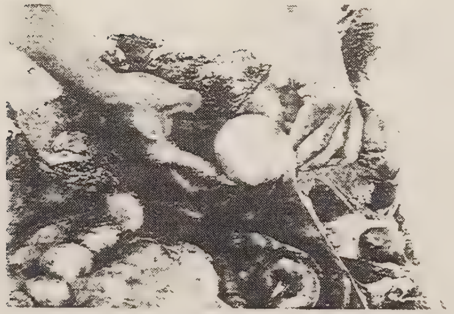

Fig. 1. Photograph of stranded leatherback, showing faecolith in situ.

At the microscopic level it could be seen that the brown material was made up of lamellae of soft material, which presumably consisted mainly of faecal bacteria (large numbers of bacteria were visible in early 'dirty' SEM preparations of the faecolith crystals). Between each of the lamellae were huge numbers of crystals (ca. 0.2-0.3 mm length, flattened and coffin-shaped). The crystals were transparent, colourless, hard, brittle and apparently insoluble in water.

## FAECOLITH CRYSTAL COMPOSITION

First, it was noticed that the crystals prepared for X-ray microanalysis by freeze-drying appeared white and chalky rather than transparent; this indicated that the original crystals contained water of crystallization. All ten faecolith crystals subjected to X-ray microanalysis showed very similar patterns to that shown in Fig. 2. There are three obvious peaks. The Al comes from the stub on which the crystal is mounted; the Mg and P are the major elements of the crystal itself. Particularly surprising is the low amount of Ca; the faecolith was clearly not calcified.

X-ray microanalysis is largely qualitative, and calculation of peak areas yields only semi-quantitative information (see Morgan, 1985 for discussion). However, calculation yielded the following mean compositions (SD in parentheses): Na 1.6 (0.5)%, Mg 32.2 (1.9)%, Si 0.9 (0.3)%, P 67.1 (2.3)%, Cl 0.7 (0.8)%, K 0.3 (0.5)%, Ca 2.2 (1.5)%. From these values it may be seen that virtually all of the identified elemental material present in the crystals consists of Mg and P, with some crystal surfaces (particularly clean ones with no contaminating material visible on the surface) approaching levels of 100%. The technique is not capable of detecting the presence of elements with an atomic number below 11 (e.g. C, H, I or O), so although the X-ray microanalysis results, combined with the observation of crystalline rather than amorphous structure, strongly suggest that the crystals are almost pure magnesium phosphate, the technique cannot discriminate between different types of phosphates (e.g. between various orthophosphates, some of which contain H, and pyrophosphate), and cannot eliminate the possibility of the presence of ammonium in the crystals (as in struvite, $NH_4MgPO_4.6H_20$).

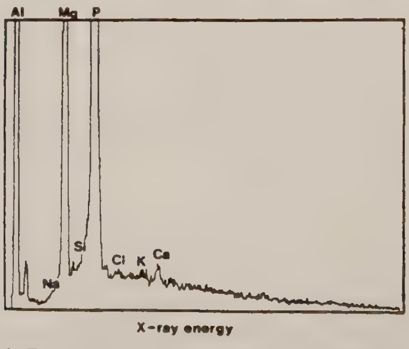

Fig. 2. Trace derived from X-ray dispersive microanalysis of faecolith crystals. Al is from the stub on which the crystal was mounted.

1. 300 mm length of tangled, blue polypropylene twine (5 mm thick).
2. 4 strands (120 mm, 105 mm, 120 mm, 130 mm) of old, unravelled polypropylene tarpaulin fabric, all 1 mm wide.
3. 160 mm length of monofilament nylon fishing line (approx. 8 lb breaking strain).
4. 4 pieces of green, hard, flat plastic (9x13 mm, 10x7 mm, 6x5 mm, 6x5 mm).
5. Piece of flat, white hard plastic (9x5 mm; 2 mm thick).
6. Piece of flat, yellow-orange hard plastic (5x5 mm).
7. 3 small strands of plastic (20 mm, 20 mm and 30 mm in length).
8. 6 small pieces (approx. 4 mm diameter) of expanded polystyrene foam.
9. Piece of unknown hard substance (6x5 mm).
10. Numerous polystyrene beads (< 1 mm diameter).
11. 3 pieces (each approx. 20 mm diameter) abraded material from polythene bags

TABLE 1. Material of anthropogenic origin incorporated in faecolith

The magnesium phosphates are all insoluble or only very slightly soluble in water, so degree of solubility cannot separate the forms, but the X-ray diffraction pattern gave a near-perfect match for struvite (JCPDS pattern number 15-762). The morphology of crystals is very similar to that recorded by LeGeros & LeGeros (1984) from struvites synthesized in gel systems. A good general description of struvite (also known as guanite) may be found in Palache *et al.* (1951).

## DISCUSSION

Faecoliths are present in some stranded leatherbacks, but certainly not all; Den Hartog & Van Nierop (1984) did not report any in the six *Dermochelys* they studied. At present it is difficult to decide whether their presence indicates a pathological condition, or is a normal feature of turtle biology. Except for the injuries caused by the shark attack, the Midway turtle showed no obvious signs of disease and there was no compaction of plastic in the gut. The adaptive formation of hard nodules in the gut of marine animals is not unknown; the heart urchin *Echinocardium* ingests fragments of wood or stone which act as a substratum for the formation of bacterial nodules which fix and detoxify sulphur as insoluble metal sulphides. There is also a general tendency in marine invertebrates for detoxification by binding metals in insoluble, granular form. It is feasible that the formation of a smooth, rounded object around non-biodegradable garbage may facilitate later defaecation. Leatherbacks not only swallow plastic bags and man-made garbage such as the twine and polystyrene reported here; they are also known to swallow wood, feathers, sand and seaweed (e.g. Brongersma, 1969; Den Hartog & Van Nierop, 1984)). It would appear that they will swallow almost any material swimming or floating at the sea surface; some of this material was presumably difficult to pass through the gut even before man started to throw non-biodegradable garbage into the sea. However, there is an extensive veterinary literature concerned with the consequences for captive animals of swallowing of foreign bodies (see Frye, 1991 for reptilian examples), but except in the case of crocodilian gastroliths (swallowed deliberately for control of buoyancy and/or digestive efficiency) the responses of animals seem to be pathological rather than adaptive. The occurrence of hard masses in the intestine of chelonians is not uncommon either (see Frank, 1981), but these are usually formed from masses of chitinous parts of insects or accumulated indigestible cellulose fibres. Such masses can cause constipation, though intestinal parasitic nematodes may help to break the masses down.

From the form of the leatherback faecolith studied here it is clear that its hardness stems from biomineralization, presumably by the gut bacteria rather than the leatherback itself, since the mineral crystals are deposited between the bacterial lamellae. It is most interesting that the mineral is non-calcareous and composed of struvite which may be formed in the laboratory by mixing magnesium sulphate solution with an acid solution of ammonium phosphate (Palache *et al.*, 1951). Struvite is not a common biomineral in a global sense, although it is well recognized in medical and veterinary circles. The principal occurrence in live organisms seems to be as a component of urinary stones in mammals (including cats and humans) resulting from alkalinization due to bacterial infection (e.g. Prien & Frundel, 1947; LeGeros & LeGeros, 1984; Lowenstam & Veiner 1989). Geological struvite occurrences have unusual bulk compositions and are non-marine (e.g. within fossil cave guano deposits); struvite has also been found in dung-peat mixtures and in canned food (Palache *et al.*, 1951). In these occurrences too, bacterial activity is probably significant.

In view of the association with bacterial lamellae in the faecolith, a similar origin seems likely in this case. A further factor may be enrichment of the hindgut fluids of the leatherback turtle by divalent ions. *Dermochelys* has to drink seawater like any other marine reptile (or teleost fish). It can only absorb water by pumping Na across the gut wall until sufficient osmotic gradient exists for water to flow osmotically from gut lumen to blood. In consequence, the hind gut fluid is likely to contain relatively high concentrations of magnesium, calcium and sulphate ions, but little sodium or chloride. However, the ammonium and phosphate ions of struvite are presumably derived from the faecal bacteria. LeGeros & LeGeros (1984) report that struvite can be formed in a calcium-rich medium at pH values between 7 and 9, and that formation of small crystals is actually promoted by high calcium concentrations, so it is not necessary to postulate a calcium-poor or acid environment in the hindgut.

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# Modeling the potential of fishery reserves for managing Pacific coral reef fishes

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**Abstract.**–The potential use of marine fishery reserves (MFRs) for managing fisheries on tropical Pacific coral reefs was assessed with an extension of the Beverton-Holt model. The effects of year-round fishery closures on harvests in adjacent, exploited areas were evaluated. Potential changes in spawning stock biomass per recruit ($SSB/R$) and yield per recruit ($Y/R$), when varying fractions of exploitable reef area were closed to fishing, were estimated from published data, approximated natural and fishing mortality rates, size- and maturity-at-age distributions, and "transfer" (emigration and immigration) rates. For select cases, fundamental transfer rates were adjusted for possible density-dependent emigration from closed areas as relative densities decreased in surrounding non-closed areas because of continued fishing. Three hypothetical "fish types" were constructed, bracketing the likely extremes in fundamental transfer rates and related life-history parameters of Pacific coral reef fishes: a small-bodied, fast-growing and short-lived, strongly philopatric species of damselfish was contrasted with a large-bodied, relatively slow-growing, long-lived, vagile species of jack. A "surgeonfish" type was used to represent intermediate parameter values.

Simulations corroborate previous observations that MFRs contribute little, if anything, towards increasing Y/R. Results for the highly vagile jack confirm that rapid transfer rates will negate potential gains in $SSB/R$ resulting from closures. At the opposite extreme, small reef philopatriots like damselfishes would almost never be harvested, because of negligible transfer rates, unless the MFR was periodically opened to fishing. The simulations suggest that the $SSB/R$ of the surgeonfish type is the most likely to benefit from MFRs, because moderate vagility allows biomass to accumulate within the closure despite harvesting in the non-closed area. Results further suggest that growth rate, fishing effort in the non-closed (open) area, natural mortality, and maturity and harvesting schedules importantly influence the potential of MFRs to augment SSB when transfer rates are low to moderate.

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Marine fishery reserves (MFRs), areas closed to harvesting and adjacent to fished areas, have recently been touted as enforceable and cost-effective alternatives to conventional fisheries management measures such as size and bag limits, closed seasons, and limited entry (Davis, 1989; Plan Development Team 1990; Polacheck, 1990; Bohnsack, in press; Davis et al.[1]; Russ et al., in press). MFRs are recognized worldwide as providing sanctuaries in which local populations of desirable species can increase in abundance or attain larger body sizes (McCormick and Choat, 1987; Alcala, 1988; Buxton and Smale, 1989; Clark et al., 1989; Russ 1985, 1989; Alcala and Russ, 1990; Cole et al., 1990; Bennett and Attwood, 1991). In contrast, harvesting is known to alter the abundance and body size distributions (Craik, 1981; Katnik, 1982; Koslow et al., 1988; Plan Development Team 1990) and assemblage structure (Bell, 1983; Russ and Alcala, 1989) of fishes on coral reefs and other localized regions of fishery exploitation.

By providing havens from exploitation within which organisms can attain large adult body sizes, designated refuges protect the most valuable segments of spawning stocks (Plan Development Team, 1990). For most marine organisms with lengthy (≥2 wk-long) planktonic larval stages, MFRs can function as sources of benthic recruits to exploited, often distant, sink populations. The subsequent contribution of these recruits to the fishery might counteract (or forestall) the effects of recruitment overfishing (Carr and Reed, in press; Russ et al., in press). Through the directed movements of settled stages, MFRs might also augment the standing biomass of stocks, including spawning adults, in exploited areas adjacent to MFRs as well as within the MFRs themselves (Polacheck, 1990; Roberts and Polunin, 1991). MFRs thus might provide a management tool that addresses growth overfishing, particularly for multispecies fisheries on tropical coral reefs where conventional management is ineffective (Roberts and Polunin, 1991).

Despite the recognized importance of MFRs as sanctuaries for conserving biomass, their contribution to fishery stocks and yields in adjacent exploited areas is poorly understood (Davis, 1989; Polacheck, 1990; Roberts and Polunin, 1991; Russ et al., in press). An introduction to the problem is provided by Polacheck (1990), who expands the Beverton-Holt equation (Beverton and Holt, 1957) describing the effects of a year-round refuge on the spawning stock biomass ($SSB$) and yield of a cohort in a surrounding exploited area. Although areal closures on coral reefs are one identified application, Polacheck's (1990, Table 1) simulations use empirical data on the growth, maturity, and harvesting schedules of Georges Bank cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*. The growth and mortality dynamics of tropical coral reef fishes, however, may be quite unlike those of higher-latitude species (Munro and Williams, 1985; Longhurst and Pauly, 1987). Further simulations using growth and mortality data of other fishes are needed.

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[1] Davis, G. E., S. C. Jameson, and J. E. Dugan. Potential benefits of harvest refugia in Channel Islands National Park and Channel Islands Marine Sanctuary. Unpubl. manuscr., 25 p. U.S. Natl. Park Service, Channel Islands National Park, CA 93001.

Observations of traditional practices by marine islanders (Johannes, 1978) suggest that reserves can augment the *SSB*, and perhaps the yield of tropical reef fishes. To date, controlled empirical measurements of fishery yields in an area adjacent to a MFR have been published for only one study site (Sumilon Island, central Philippines; Alcala and Russ, 1990). The changes in catches that Alcala and Russ (1990) observed, however, were based on yield, not yield per recruit ($Y/R$), over a 1-year period and therefore may not have represented equilibrium conditions.

The present paper evaluates the effects of permanently closed MFRs of different sizes on net changes in *SSB* and yield for several types of tropical Pacific reef fishes. The author simulated various combinations of fishing mortality and emigration-immigration ("transfer") rates for fishes having different but typical natural growth and mortality schedules. Because tropical reef fishes have higher natural growth and death rates than do temperate zone fishes, the focus is on the relative sensitivity of spawning stock biomass per recruit ($SSB/R$) and $Y/R$ to MFR size, transfer rates, variations in natural mortality and growth, fishing effort, and age at first capture. Another objective is to compare the management potential of "single large or several small" (SLOSS) (Simberloff, 1988) reserves of equal total area. Finally, the potential of MFRs on island reefs is discussed, with particular reference to reef areas surrounding the island of Oahu, Hawaii.

## Methods

Parameter values for von Bertalanffy growth rates, derived mortality rates, and maturity and harvesting schedules were chosen to bracket the spectrum of life histories and exploitation characteristics of tropical Pacific reef fishes. At one extreme, values were assembled to describe a reef transient (e.g., a jack of the family Carangidae) that is relatively slow-growing but long-lived and large-bodied is likely to travel rapidly over relatively large distances. Such species often support valuable commercial fisheries. Values used for growth and mortality rates of the jack resemble those of many species of commercially important snappers, groupers, and jacks from the South Pacific and other tropical seas (Munro, 1983; Munro and Williams, 1985).

A short-lived, fast-growing but small-bodied reef damselfish (family Pomacentridae), with limited movements after settlement, was used to represent the opposite extreme. Such small tropical reef species are collected for the aquarium fish trade.

In between these two extremes lies a broad continuum of fishes with intermediate longevities, body sizes, and movement rates. These fishes probably represent most species targeted by recreational and artisanal fisheries on tropical reefs. The few data available (Galzin, 1987; Ralston and Williams[2]; Russ and St. John, 1988; Dalzell, 1989) suggested a range of moderate growth and mortality rates for a number of Pacific parrotfishes (family Scaridae) and surgeonfishes (family Acanthuridae). For convenience, these fishes were labeled the "surgeonfish" type.

The growth parameters used in this study were based partly on published values for a particular species population, complemented by data for other Pacific populations of the same species. For the pomacentrid, the author used a Moorean population of *Stegastes nigricans* (Galzin, 1987). He selected *Ctenochaetus striatus* as the surgeonfish; the length-weight relation was based on a Moorean population (Galzin, 1987), and a Samoan population provided the VBGF parameters (Ralston and Williams, 1988). Sudekum et al.'s (1991) data for NWHI *Caranx ignobilis* were used to represent the jack. Thus the degree to which values were population-specific varied among the three fish types. Natural mortality rates ($M$) were estimated using Pauly's (1980) multiple regression of $M$ on maximum size, growth coefficient, and mean water temperature (Pauly and Ingles, 1981); 25°C was chosen as representative for shallow, tropical Pacific waters. All parameter values used are listed by fish type in Tables 1 and 2.

### Modeling closure effects

Polacheck's (1990) model of the effects of closure size (1–50%), rates of fish transfer between closed and exploited areas, and fishing mortality rate on the biomass and production of fishes in an adjacent exploited area was used with one small but important difference: the use of a three- rather than a four-sided closed area. (Closures on island reefs usually extend seaward from the shoreline, so fishes can move across upcoast, downcoast, and offshore boundaries only. Other factors being equal, dispersion rates out of and into shore-

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[2] Ralston, S., and H. A. Williams. 1988. Age and growth of *Lutjanus kasmira, Lethrinus rubrioperculatus, Acanthurus lineatus*, and *Ctenochaetus striatus* from American Samoa. Dep. of Commer., Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. H-88-18, 11 p.

### Table 1

Length-weight relations, von Bertalanffy growth function parameters, and natural mortality rates used to simulate spawning stock biomass per recruit and yield per recruit contour surfaces for damselfish (based on Moorean *Stegastes nigricans* from Galzin, 1987); surgeonfish (length-weight relation: Moorean *Ctenochaetus striatus* from Galzin, 1987; VBGF parameters: Samoan *C. striatus* from Ralston and Williams[2]); and jack (NWHI *Caranx ignobilis* from Sudekum et al., 1991). *M* values were estimated after Pauly (1980) and Pauly and Ingles (1981; see Methods).

| Variable | Damselfish | Surgeonfish | Jack |
|---|---|---|---|
| Length-weight relation (Total Length/g) | $W = 0.0195L^{3.07}$ | $W = 0.0111L^{3.10}$ | $W = 0.0072L^{2.98}$ |
| $L_\infty$ (Total Length, cm) | 17.5 | 28.2 | 217 |
| $W_\infty$ (g) | 128.9 | 348.6 | 120,139 |
| $K$ (1/year) | 0.374 | 0.447 | 0.111 |
| $t_0$ (year) | –0.042 | –0.760 | –0.097 |
| $M$ (1/year) | 1.5 | 1.0 | 0.2 |

### Table 2

Age-specific parameters used to simulate the standing stock and catch (yield) values for each of the reef fish types described in Table 1.

| Fish type | Age (yr) | Mean weight[1] (g) | Percent mature[2] | Partial recruitment[3] |
|---|---|---|---|---|
| Damselfish | 1.0 | 4.77 | 100 | 1.00 |
| | 2.0 | 32.40 | 100 | 1.00 |
| | 3.0 | 72.20 | 100 | 1.00 |
| Surgeonfish | 1.0 | 40.81 | 0 | 0 |
| | 2.0 | 101.87 | 100 | 1.00 |
| | 3.0 | 164.43 | 100 | 1.00 |
| | 4.0 | 217.18 | 100 | 1.00 |
| | 5.0 | 257.24 | 100 | 1.00 |
| Jack | 1.0 | 110.0 | 0 | 0 |
| | 2.0 | 861.7 | 0 | 0 |
| | 3.0 | 2587.0 | 0 | 0 |
| | 4.0 | 5348.6 | 100 | 1.00 |
| | 5.0 | 9061.8 | 100 | 1.00 |
| | 6.0 | 13,569.6 | 100 | 1.00 |
| | 7.0 | 18,688.4 | 100 | 1.00 |
| | 8.0 | 24,235.1 | 100 | 1.00 |
| | 9.0 | 30,042.0 | 100 | 1.00 |
| | 10.0 | 35,963.5 | 100 | 1.00 |
| | 11.0 | 41,878.8 | 100 | 1.00 |
| | 12.0 | 47,691.4 | 100 | 1.00 |
| | 13.0 | 53,327.1 | 100 | 1.00 |
| | 14.0 | 58,731.1 | 100 | 1.00 |
| | 15.0 | 63,865.3 | 100 | 1.00 |

[1] Based on mean weight-at-age estimated from weight-specific VBGF; see Table 1 for sources.

[2] Sexual maturity assumed 100% complete at age corresponding to the asymptote of the Von Bertalanffy growth function curve; all fish were assumed immature prior to this age.

[3] All species were defined as fully recruited to the fishery at the age of 100% sexual maturity, no fish entering the fishery prior to that age: Age-at-first-capture, $A_c$ = 1.0, 2.0, and 4.0 years for the damselfish, surgeonfish, and jack, respectively.

line-bounded reef closures will be one-fourth slower than the respective rates for completely nested closures of equal areal extent.)

Polacheck's modified Equation 8 was

$$T_{12} = 3 \cdot T_{1s} \cdot (R_1 / R_s)^{-1/2}; \qquad (1)$$

where $T_{12}$ is the instantaneous emigration rate from closed area 1 to exploited area 2; $T_{1s}$ is the emigration rate from a closure of $R_s$ standard size; and $R_1$ is the fractional closure size evaluated. As in Polacheck (1990), the initial fish densities were assumed homogeneous in both areas, and thus the number of fish initially present in area 1 at time $t$ was defined as

$$N_{1,t} = R_1 \cdot N_{total,t} \qquad (2)$$

where $N_{total,t}$ = number of individuals in the cohort entering areas 1 and 2 at time $t$. $T_{1s}$ was allowed to vary among fish types, as types surely differ in their fundamental emigration and immigration rates. Selected values of $T_{1s}$ spanned realistic values for each fish type (damselfish: 0.001, 0.01, and 0.1; surgeonfish: 0.1, 0.25, and 0.5; jack: 0.1, 0.5, and 1.0). $T_{21}$, the rate of immigration into area 1 from area 2, given the type-specific value of $T_{1s}$, was as defined by Polacheck (1990, Equation 6).

A basic assumption of the model is that fishing does not affect fish distributions by altering habitat or by promoting density gradients between areas 1 and 2, i.e., dispersal is random and uniform throughout both areas and across their boundaries (Polacheck, 1990). This is realistic for fishes like jacks that range widely or that have very large home ranges. However, the assumption of uniform dispersal throughout both areas is debatable for fishes with home ranges that are small relative to the size of MFRs, particularly for strongly site-attached, territorial species like damselfishes whose ambits are trivial compared to the area of a reserve. Transfer rates that functionally approximate those based on an assumption of uniform, random dispersal might be tenable for home-ranging (or even territorial) organisms, if emigration out of MFRs into adjacent fished areas followed a "stepping stone" pattern with minimal time lags. Limited field data at present both support (Walsh, 1984) and counter (Wellington and Victor, 1988) such a model. The key factors here are the magnitude of time lags and the relative sizes of individual home ranges within particular MFRs.

An $R_s$ value of 0.10 was used to represent the "standard-size" closure (Polacheck, 1990). Fishing mortality rates ($F_c$) were input over the range from 0.1 to $\geq 3M$, with special evaluation of $F_c = 0.5M$, $M$, and $2M$, based on the best estimate of natural mortality for each fish type. Total fishing effort ($F_2$) was homogeneously redistributed throughout the exploited area and fixed in magnitude (at a given $F_c$), regardless of the size of the closed area (Equation 7 in Polacheck, 1990).

*SSB*/*R* and *Y*/*R* are used as the primary bases of evaluation. Although measures of biomass are not usually applicable to species like the damselfish that are harvested on a numerical basis (see Ingles and Pauly [1984] for examples of consumptive exploitation of small-bodied fishes in artisanal fisheries), these measures were evaluated in the same way to maintain consistency.

First, the *SSB* and yield of a cohort were calculated, by using Polacheck's (1990) Equations 2 and 3 for the numerical standing stock and the numerical catch of each cohort comprising that stock:

$$\sum_{(t=1)}^{n} (N_{1,t+1} \cdot \bar{W}_{t+1} \cdot \%\mathrm{mat}_{t+1}), \tag{3}$$

$$\sum_{(t=1)}^{n} (N_{2,t+1} \cdot \bar{W}_{t+1} \cdot \%\mathrm{mat}_{t+1}), \text{ and} \tag{4}$$

$$\sum_{(t=1)}^{n} (C_{2,t} \cdot \bar{W}_t); \tag{5}$$

where $N_{1,t+1}$ and $N_{2,t+1}$ are the numbers of a cohort surviving in the respective area at time $(t+1)$; $C_{2,t}$ is the numerical catch of a cohort in area 2 at time $t$; $\bar{W}_t$ and $\bar{W}_{t+1}$ represent the mean weights of individual fish of the cohort at times $t$ and $(t+1)$, respectively; and $\%\mathrm{mat}_{t+1}$ is the percentage of the cohort that is sexually mature at time $(t+1)$.

*SSB*/*R* and *Y*/*R* were then calculated by standardizing the total spawning biomass and yield, respectively, of the cohort over its life span by the total number of recruits potentially (area 1) and directly (area 2) entering the fishery from that cohort (Gabriel et al., 1989). *SSB*/*R* was evaluated in terms of percentage of the virgin stock biomass possible if fishing was disallowed in both areas (Polacheck, 1990); 20% of virgin biomass was considered the threshold for recruitment overfishing (Beddington and Cooke, 1983).

Two series of simulations were run. One series treated the $T_{12}$ and $T_{21}$ values as fixed, assuming that, analogous to Polacheck's (1990) analyses for Georges Bank cod, transfer rates would remain constant and independent of relative fish densities in the two areas. Additional simulations, using the same initial $T_{1s}$ values, were run for selected cases; in these runs, subsequent values of the transfer rates were treated as a density-dependent function of the changing, relative fish densities in the two areas. Subsequent values of $T_{12}$ and $T_{21}$ were adjusted as follows:

$$T_{12,t+1} = T_{12,t} \cdot \{ (N_{1,t}/N_1) / (N_{2,t}/N_2) \}^x, \text{ and} \tag{6}$$

$$T_{21,t+1} = T_{21,t} \cdot \{ (N_{2,t}/N_2) / (N_{1,t}/N_1) \}^x; \tag{7}$$

where $N_1$ is defined in Equation 2 and $N_2$ is the initial number of the cohort present in area 2; $N_{1,t}$ and $N_{2,t}$ are the numbers of fish surviving in the respective area at subsequent age $t$; and $x$ is the power used to scale the ratio of fish densities. In Equations 6 and 7, the ratio of the numbers of fish surviving at time $t$ was further adjusted by the ratio of initial densities in the two areas in order to scale for the propensity to emigrate at the onset. Two values of $x$ were evaluated: 0.125 (eighth root) and 0.5 (square root). (Note: When $x$ equals 0, the $T_{12}$ and $T_{21}$ are fixed; when $x$ equals 1.0, these rates are continually readjusted by the changing ratio of relative densities.) Exponents of 0.125 and 0.5 were chosen because they bracketed rate changes of reasonable magnitude. In the surgeonfish, for example, an eighth-root adjustment would initially accelerate a median $T_{1s}$ of 0.25 by about 20% for a median closure size of 25%, at an $F_c$ of 1.0. The corresponding rate increase due to a square-root adjustment would be 60%.

Inclusion of a term for the density-dependent adjustment of transfer rates, as stocks are fished-down in the non-closed area, extends Polacheck's (1990) evaluation. This is perhaps an unnecessary refinement for stocks such as Georges Bank cod for which harvesting by trawl might reduce habitat quality in the non-closed area (Polacheck, 1990). However, non-destructive (e.g., hook and line) methods of artisanal fisheries on coral reefs do not reduce habitat quality. Furthermore, fishes may emigrate at an accelerated rate from a closure into the surrounding non-closed area where densities continue to decrease (tantamount to improving habitat quality). Compensatory emigration resulting from a density gradient is recognized as potentially important in the siting and design of nature reserves (Schonewald-Cox and Bayless, 1986).

## Complementary simulations

In addition, the effects of varying $M$ and the age-at-first capture ($A_c$) on total biomass per recruit ($B/R$) were simulated with the conventional $Y/R$ model of Beverton-Holt (Sparre et al., 1989). Fishing mortality was evaluated at $0.5M$, $M$, and $1.5M$ or $2M$. $A_c$ was examined with the most reasonable estimate of $A_c \pm 50\%$ for each of the three fish types (see footnote C of Table 2 for the type-specific values of $A_c$ used in modeling closure effects). An age-at-recruitment to fishery habitat ($A_r$) value of 1.0 year was assumed for the surgeonfish and jack, and an $A_r$ of 0.5 year for the damselfish.

## Results

### General

Results corroborate several of Polacheck's (1990) major results: *SSB/R* increased, while *Y/R* generally decreased, with increasing refuge size (Fig. 1). Even in cases where a closure positively affected yield, *Y/R* increased little. *Y/R* often was greater at higher levels of fishing effort (Fig. 1) and usually decreased at larger refuge sizes; the rate of decrease was less at higher fundamental transfer rates (Fig. 2, A–C). *SSB/R* was generally greater for closures of larger size at any particular transfer rate (Figs. 1 and 2). The positive effects of a closure of a given size on *SSB/R* were greater at lower rates of exploitation and diminished at higher transfer rates (Fig. 3). The rate of increase in *SSB/R* with refuge size was greater at lower transfer rates (Fig. 1, A–C). The progressive gain in *SSB/R* usually was greater than the progressive loss in *Y/R* for refuges of increasing size (Fig. 2).

Another general pattern was the relative importance of the interactive effect of natural and fishing mortality rates, compared to age at recruitment to the fishery. For most combinations of $M$ and $F_c$, *B/R* was more strongly influenced by these two rates than by age at recruitment (Fig. 4, Table 3). Depending on fish type, *B/R* values ranged two- to five-fold as $M$ and $F_c$ values varied ±50% of their midpoint estimates, but ranged only twofold or less as $A_c$ varied ±50% (Table 3).

By comparison, transfer rates had relatively little effect on *SSB/R*, compared with the effects of natural and fishing mortality rates. For a median-sized closure of 25%, changes in percentage of virgin *SSB/R* differed <10% within fish type for transfer rates that varied as much as two orders of magnitude (Fig. 3).

Another generality, not previously made explicit, is that ages at maturity and at first capture can more strongly influence spawning stock than can the presence and size of a refuge. The presence of a refuge will have a relatively weak effect on spawning biomass if the resource begins to be heavily exploited well before sexual maturity. In extreme cases, *SSB/R* might not be appreciably enhanced by large closures, despite relatively low transfer rates.

### Fish types

Perhaps the most significant, specific result of the simulations was that fish types differed in how refuge size affected *SSB/R* levels. Large, apparent gains in percent virgin *SSB/R* of the damselfish occurred only at the expense of large losses in yield (Figs. 1A, 2A, 3A). Nontrivial (>5%) gains in percentage *SSB/R* of surgeonfish could occur at small (0.1) refuge sizes, although the overall rate of increase in *SSB/R* would be greater for larger closures (Figs. 1B, 3B). For the jack, however, gains in *SSB/R* of magnitude similar to those of the surgeonfish could be realized with increasing refuge size only for large ($R_1 > 0.3$) closures (Figs. 1C, 3C).

Simulation results appeared to vary among fish types in response to their differing growth rates and natural mortality and exploitation schedules. For example, in comparing the results for the high-mortality surgeonfish with those for the low-mortality jack, substantive gains in *SSB/R* of the jack (restricted to large closures) were further restricted to low ($F_c \le 0.4$) levels of fishing effort (Fig. 1C). *SSB/R* dropped below 20% of the virgin stock at $F_c = 0.3$, the fishing effort that was optimal for maximizing *Y/R* (Fig. 1C). For the surgeonfish, appreciable (≥10%) gains in *SSB/R* could occur under heavy ($F_c > 1$) exploitation rates for refuges as small as 10–20% (Fig. 3B), and ≥20% of virgin *SSB/R* can be sustained at $F_c \le 1.15$ (Fig. 1B).

The observed differences among fish types in the potential for MFRs to increase *SSB/R* also were strongly influenced by the ages at sexual maturity and recruitment to the fishery. Ages at first maturity and at first capture were attributes that differed greatly among the three fish types (damselfish: age 1; surgeonfish: age 2; jack: age 4; Table 2). Median *B/R* (equal to *SSB/R* for all except the damselfish at $A_c$ = 0.5 year) varied by 30% for the damselfish, 100% for surgeonfish, and 35% for the jack among ages at first capture that varied ±50% of their respective midpoints (Table 3). Compared with age at first catch, transfer rates had less effect; *SSB/R* consistently varied ≤10% for the damselfish (with twofold variation in very low transfer rates; Fig. 3A), for the surgeonfish (with fivefold variation in moderate transfer rates; Fig. 3B), and for the jack (with tenfold variation in rapid transfer rates; Fig. 3C). At a reference $F_c$ of 1.0 and a median closure size of 25%, *SSB/R* varied from <6 to 35% of virgin stock biomass, depending on fish type (Fig. 1, A–C).

### Compensatory transfer rates

Even small (eighth root of density ratio) compensatory increases in transfer rates could have negated potential increases in *SSB/R* that might result from the presence of a closure. A larger adjustment with the square root of the density ratio, of course, can have an

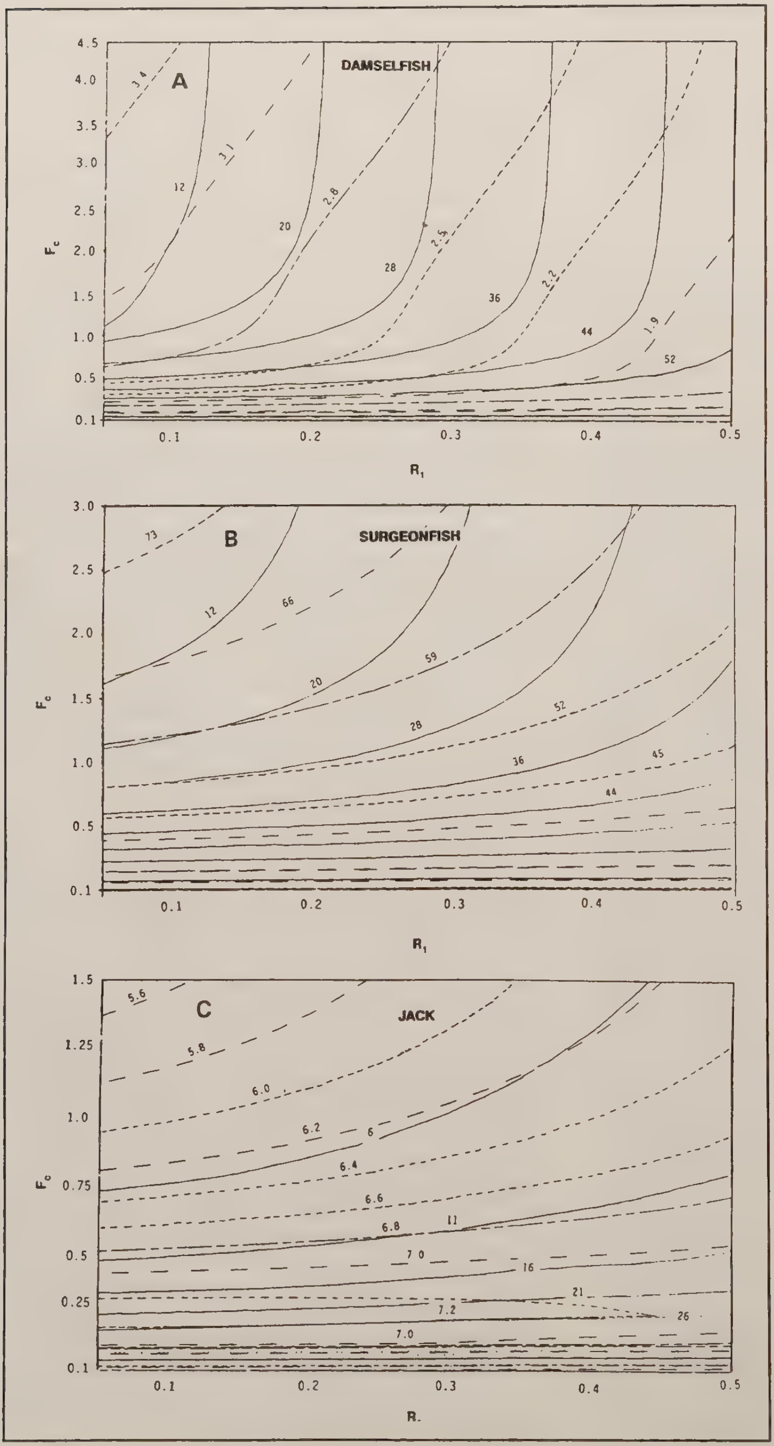
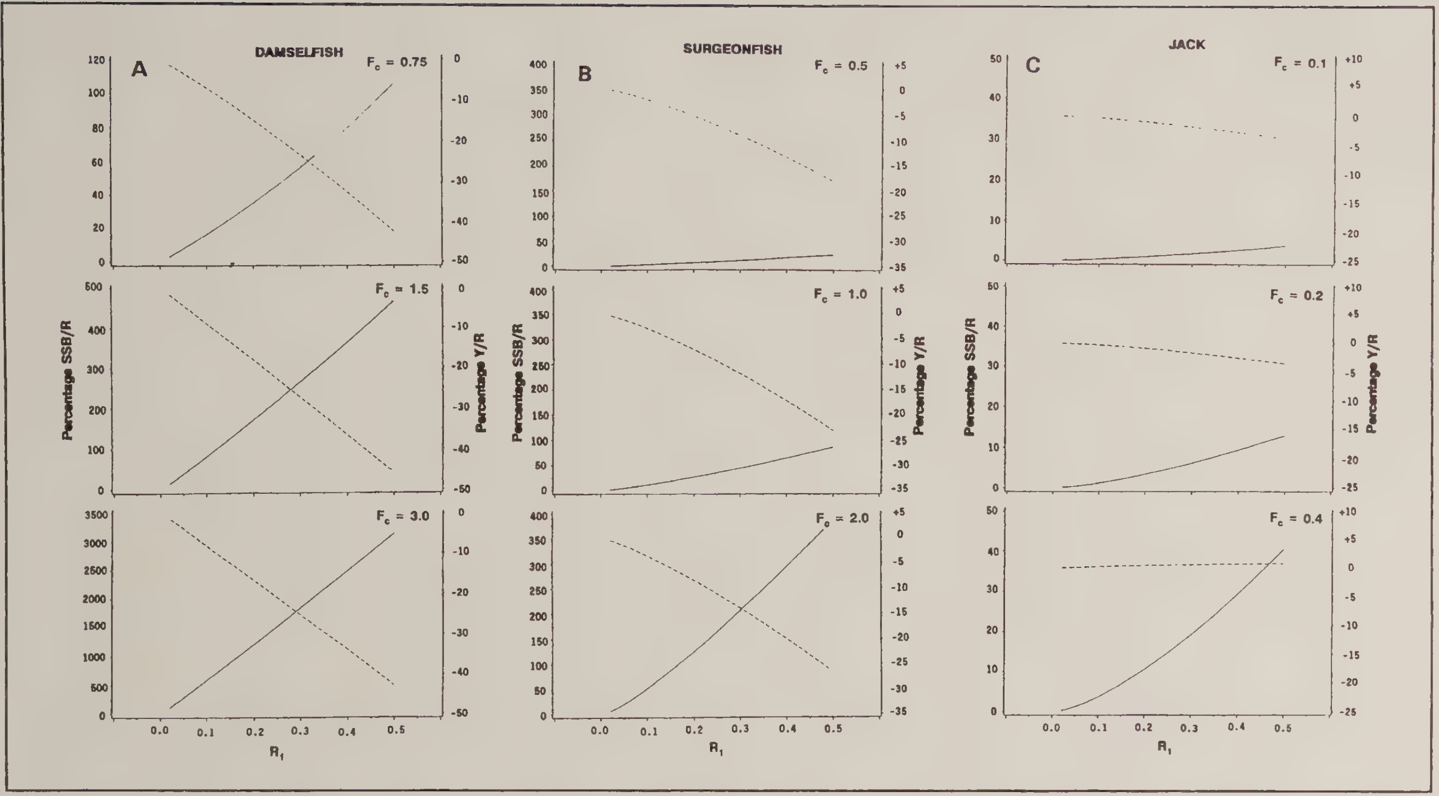


**Figure 1**

Overlay of a yield-per-recruit surface (various dashed lines) on a percentage spawning stock biomass-per-recruit surface (solid lines) as a function of refuge size ($R_l$) and fishing mortality rate ($F_c$) when transfer rate ($T_{1s}$) is constant: (**A**) damselfish ($T_{1s}$ = 0.01); (**B**) surgeonfish ($T_{1s}$ = 0.25); and (**C**) the jack ($T_{1s}$ = 0.5). Spawning biomass values are expressed as a percentage of virgin biomass that would accrue if no fishing were allowed in areas 1 and 2.



## Figure 2

Percentage changes in spawning stock biomass per recruit (*SSB/R*; solid line) and yield per recruit (*Y/R*; dashed line) as a function of refuge size ($R_1$), when transfer rate ($T_{1s}$) is constant, for different fishing mortality rates ($F_c$): **(A)** damselfish ($T_{1s}$ = 0.01); **(B)** surgeonfish ($T_{1s}$ = 0.25), and **(C)** the jack ($T_{1s}$ = 0.5). Spawning biomass and yield values are standardized by the biomass and yield that would accrue if there were no closure (i.e., both areas 1 and 2 open).

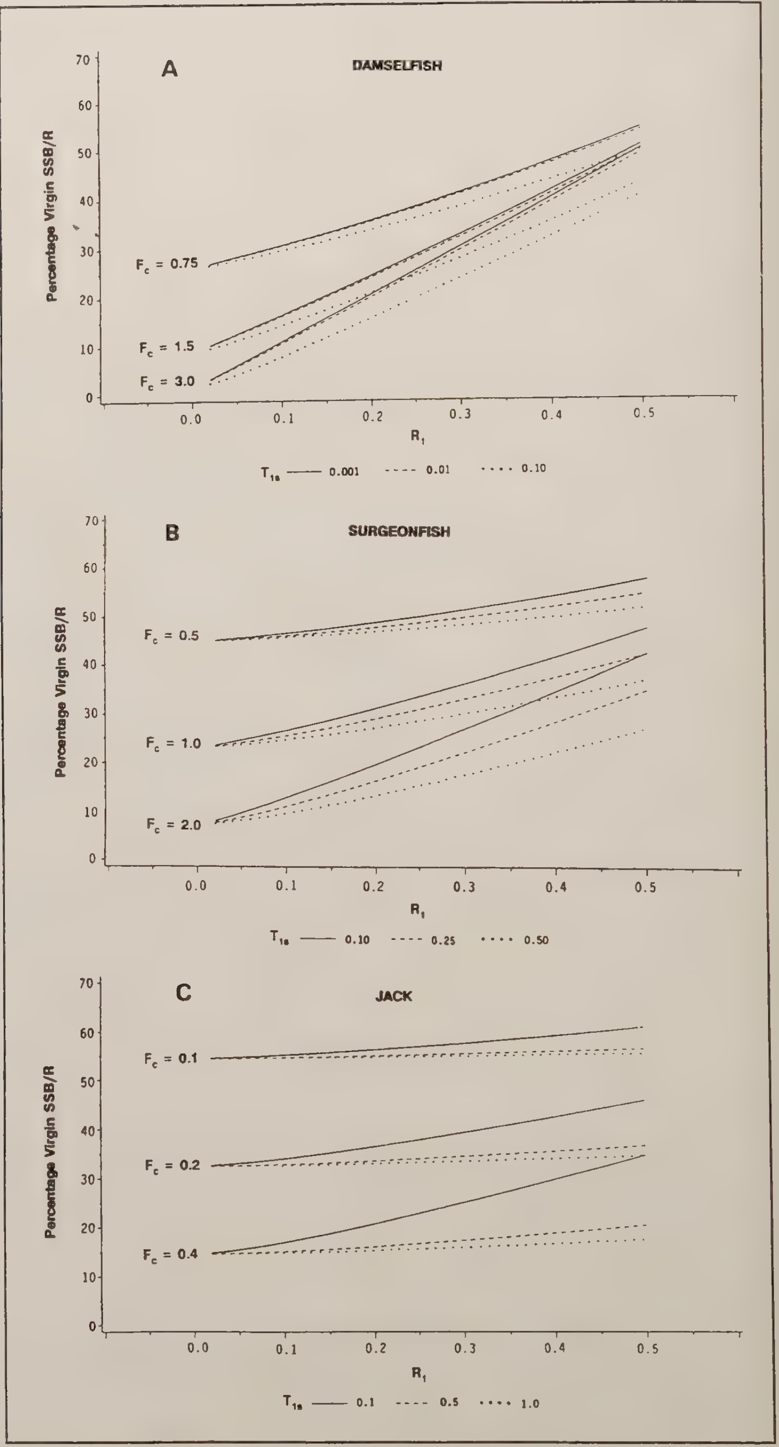


**Figure 3**

Relative changes in spawning stock biomass per recruit ($SSB/R$) as a function of refuge size ($R_1$) compared at fishing mortality rates ($F_c$) equal to natural mortality rates ($M$) of $0.5M$, $M$, and $2M$, among a range of possible fundamental transfer rates ($T_{1s}$) for (**A**) damselfish (in grams), (**B**) surgeonfish (in grams), and (**C**) the jack (in kilograms). $SSB/R$ values are standardized by the respective virgin biomass value that would accrue if no fishing were allowed in areas 1 and 2.

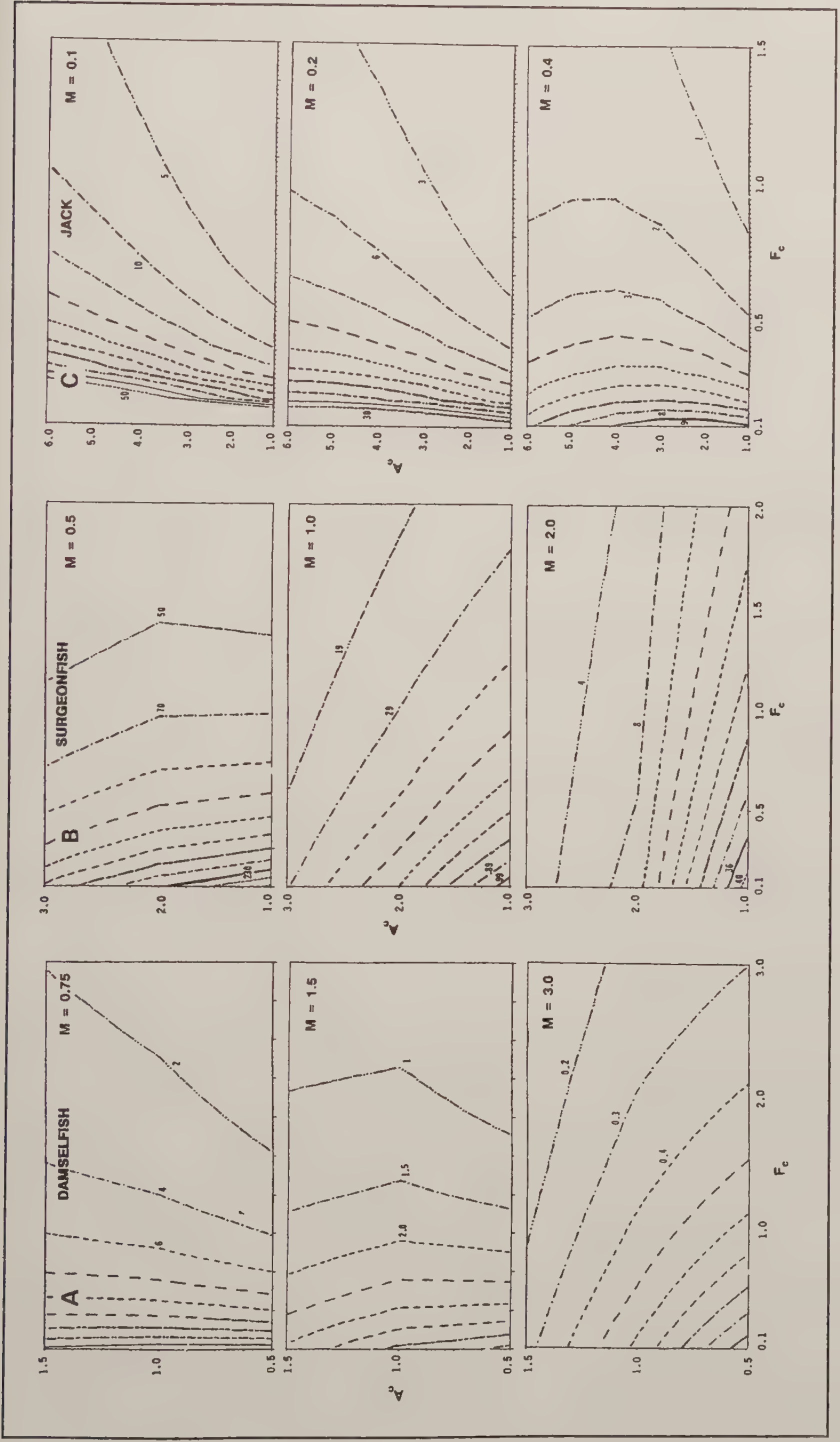


Figure 4

Stock biomass per recruit ($B/R$) surfaces as a function of fishing mortality rates ($F_c$) and age-at-recruitment to the fishery ($A_c$) for (**A**) damselfish (in grams), (**B**) surgeonfish (in grams), and (**C**) the jack (in kilograms).

Table 3

Equilibrium $B/R$ (total biomass per recruit) values without any refuge at select combinations of $A_c$ (age-at-first-capture), $M$ (natural mortality rate), and $F_c$ (fishing mortality rate) for each of the three fish types. See text Methods, Table 1, and footnotes to Table 2 for basis of chosen $A_c$ and $M$ values. $F_c$ was evaluated at values equal to $0.5M$, $M$, and $1.5M$. $B/R$ at the most reasonable (midpoint) values of $A_c$ and $M$ are emphasized in bold and underlined type, respectively, and the relative influences of $A_c$, $M$, and $F_c$ on $B/R$ are noted. $A_r = 0.5$ year (damselfish) and 1.0 year (surgeonfish and jack).

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Damselfish** $B/R$ (g) | | | | | | | | |
| | $A_c = 0.5$ | | | **$A_c = 1.0$** | | | $A_c = 1.5$ | | |
| At $M$ = | 0.75 | 1.5 | 2.25 | 0.75 | 1.5 | 2.25 | 0.75 | 1.5 | 2.25 |
| If $F_c$ = 0.75 | 5.4 | 2.1 | 1.1 | **6.7** | **2.3** | **1.0** | 7.4 | 1.9 | 0.6 |
| 1.50 | 2.1 | 1.1 | 0.7 | **3.3** | **1.4** | **0.7** | 4.0 | 1.2 | 0.4 |
| 2.25 | 1.1 | 0.7 | 0.5 | **2.0** | **1.0** | **0.5** | 2.6 | 0.9 | 0.3 |
| | $M = F_c >> A_c$ | | | | | | | | |
| | **Surgeonfish** $B/R$ (g) | | | | | | | | |
| | $A_c = 1.0$ | | | **$A_c = 2.0$** | | | $A_c = 3.0$ | | |
| At $M$ = | 0.5 | 1.0 | 1.5 | 0.5 | 1.0 | 1.5 | 0.5 | 1.0 | 1.5 |
| If $F_c$ = 0.50 | 119.9 | 66.8 | 44.8 | **110.0** | **40.5** | **17.4** | 85.4 | 19.9 | 5.3 |
| 1.00 | 66.8 | 44.8 | 33.2 | **66.7** | **28.7** | **13.4** | 54.0 | 14.4 | 4.2 |
| 1.50 | 44.8 | 33.2 | 26.2 | **47.3** | **22.1** | **10.9** | 39.2 | 11.3 | 3.4 |
| | $M > F_c = A_c$ | | | | | | | | |
| | **Jack** $B/R$ (kg) | | | | | | | | |
| | $A_c = 2.0$ | | | **$A_c = 4.0$** | | | $A_c = 6.0$ | | |
| At $M$ = | 0.1 | 0.2 | 0.3 | 0.1 | 0.2 | 0.3 | 0.1 | 0.2 | 0.3 |
| If $F_c$ = 0.1 | 96.4 | 36.6 | 17.6 | **112.3** | **40.3** | **18.0** | 123.0 | 39.8 | 15.6 |
| 0.2 | 40.4 | 19.4 | 10.8 | **54.5** | **24.3** | **12.2** | 65.6 | 25.8 | 11.3 |
| 0.3 | 21.5 | 11.9 | 7.3 | **32.8** | **16.5** | **9.0** | 42.5 | 18.6 | 8.7 |
| | $M > F_c > A_c$ | | | | | | | | |

even larger countering effect (Fig. 5). The effect of compensatory rate adjustments apparently varied with fish type in a manner not directly related to fundamental transfer rate. When the surgeonfish and jack were each evaluated using $T_{1s} = 0.1$ as the fundamental rate, compensatory dampening in the rate of $SSB/R$ gain at larger refuge sizes was less for the surgeonfish (Fig. 5A) than for the jack (Fig. 5B).

## Discussion

### MFRs and enhanced Y/R

Simulations to date suggest that MFRs have the potential to augment $SSB/R$, but enhance $Y/R$ little, if at all, in adjacent non-closed areas (Polacheck, 1990; the present study). The only empirical study to date was inconclusive: Alcala and Russ's (1990) observations of an effect on reef fish catches adjacent to the Sumilon Island reserve were from a series of years in which the reserve operated and from only one year of reduced catches that began 18 months after the reserve's protected status ended. Catches were dominated by one taxon (fusiliers, family Caesionidae; 65% of total) that used the reef for nocturnal shelter but whose zooplankton prey may have been unrelated to reef area (Alcala and Russ, 1990). Brief changes in yield, rather than $Y/R$, particularly on a small (0.5 km$^2$) spatial scale, may represent nonequilibrium phenomena (e.g., lagged effects on adult abundance resulting from a localized change in recruitment). Alcala and Russ's (1990) observations therefore are not necessarily inconsistent with simulation results (see Russ et al., in press).

Clearly, additional empirical measures are needed for $Y/R$ as well as $SSB/R$ of fishery resources in exploited regions adjacent to MFRs. For the present discussion, however, this paper will focus on simulated $SSB/R$ results.

### Relative influences of input parameters

Growth rate is a major influence of biomass accrual within refuges (Polacheck, 1990), as fast-growing fish can elaborate more surplus production (yield) per unit time and unit area of refuge than can slow-growing fish. And since growth and mortality rates are linked, it is not surprising that mortality rate is important, as fishes with a higher natural mortality can support fisheries in which they are harvested more heavily and earlier in life than can fishes with a lower mortality rate.

In the basic yield model, the effects of natural mortality and level of exploitation overwhelm those of age at first capture. Proportional changes in rates obviously have larger effects than equal-sized changes in the time period over which the rates apply. Of greater interest here are the relative magnitudes of the effects

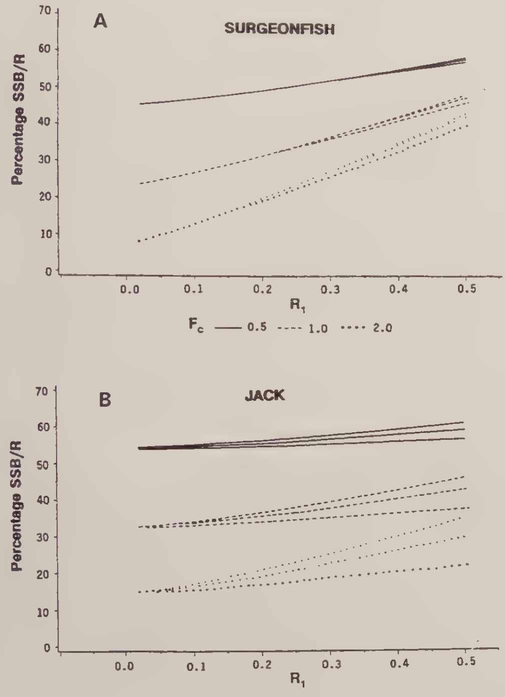


**Figure 5**

Percentage changes in spawning stock biomass per recruit (*SSB/R*) as a function of refuge size ($R_1$), fundamental transfer rate ($T_{1s}$), and two levels of density-dependent, compensatory adjustment of this fundamental rate: (**A**) surgeonfish ($T_{1s}$ = 0.1); (**B**) jack ($T_{1s}$ = 0.1). Within each triplet of lines, the upper, middle, and lower line depicts the unadjusted, adjusted 0.125-power, and adjusted 0.5-power rate, respectively.

of ages at sexual maturity and first capture, versus those of refuge size and transfer rates. I suggest that the former can have large influences for relatively short-lived, fast-growing species like the surgeonfish for which changes in age at first capture of only ±1 year represent a large fraction of its life span.

Circumstantial evidence suggests that the relative ages at sexual maturity and first capture can be important. Prior evaluations of the potential for MFRs to conserve the *SSB* of overfished commercial stocks (e.g., red snapper, *Lutjanus campechanus*) have concurrently considered other management safeguards, such as size limits in the non-closed area (Plan Development Team, 1990). However, nearshore reef fishes subject to recreational harvest are often fished at sizes and ages considerably less than those at sexual maturity, even on moderately populated islands (e.g., the island of Hawaii; Hayes et al., 1982). For reef fishes near densely populated areas where exploitation is likely to be intense on pre-reproductive fish, the potential for MFRs to enhance *SSB/R* may be severely compromised, even at closure sizes that are as large as is practical (e.g., 25%).

### Compensatory emigration

Density-dependent increases in the fundamental transfer rate can in essence depress potential gains in *SSB/R* in a manner analogous to that of a higher but constant fundamental transfer rate. The observation that gains in *SSB/R* at increasingly large refuge sizes were strongly offset by compensatory movements in the jack, but not in the surgeonfish, perhaps reflects the jack's slower growth rate, greater longevity, and lower mortality rate. Longevity, per se, may be important, because the model that was used to describe compensatory emigration is dependent upon time as well as age.

### SLOSS effects on MFR function

Simberloff (1988) reviewed the SLOSS concept and the meager results to date regarding whether multiple, small reserves function the same as single reserves of equal total size. Historically the issue of SLOSS has been applied to the preservation of threatened and endangered species or the conservation of biotic diversity (Bell and Boecklen, 1990, but see Goeden, 1979). It is increasingly apparent that meaningful stewardship of the environment and its biota extends beyond these simple (although often difficult to implement) criteria. Overexploiting an ecosystem's productivity by overfishing (Russ, 1991) is just as detrimental as recruitment or growth overfishing.

Bohnsack (1991) recently applied the SLOSS concept in a review of the function of artificial reefs. Obviously MFRs also can be evaluated in terms of SLOSS—the question then may be, "Do several small reserves potentially enhance *SSB/R* to the same extent as one reserve of equivalent total size?" A realistic example may be the relative fishery enhancement potential of ten 1% closures versus one 10% closure. Establishing a MFR of 10% may be impossible on a heavily populated island (like Oahu, Hawaii) where shoreline development is near saturation. The siting of multiple, smaller refuges, each about 1% of the total area, may be feasible, however. But can a total closure of realistic size (10%) be beneficial, and can the potential of ten 1% closures approximate it?

The simulation results suggest that a total closure of 10% may enhance the spawning stock of a fast-growing, moderately vagile reef species such as surgeonfish: at a fishing mortality rate ($F_c$) of 1.0 (equal to $M = 1.0$), $SSB/R$ can be increased by about 24% over the no-closure case for an MFR of 10%, if the lower bound of $T_{1s}$ (0.10) is used as the fundamental emigration rate. By using the higher bound for $T_{1s}$ (0.5) and an $F_c$ still at 1.0, $SSB/R$ is increased by 12% for the single 10% closure.

The overall contribution of multiple, small closures will be less, however, than that of one closure of equal total size, in inverse proportion to the increase in the total perimeter of (hence dispersal from) the multiple closures. (This follows from the general rule that smaller reserves have greater perimeter-to-area ratios than larger reserves of equivalent shape [Schonewald-Cox and Bayless, 1986].) In our example, the total perimeter of ten 1% closures is about three times ($\sqrt{10}$) that of one 10% closure. Hence, for a given fundamental transfer rate, the actual transfer rate will be appreciably greater, and the additive contribution of ten 1% closures to $SSB/R$ will be several times less, than that of one 10% closure. Multiple 1% closures might translate to an actual emigration rate approaching 0.5 for a surgeonfish that is moderately vagile ($T_{1s}$ = 0.1–0.25) relative to an MFR of 10%.

For the preceding arguments to hold, we must further assume that the multiple closures will not interact spatially. It seems reasonable though that for post-settlement stages of species with low fundamental transfer rates, ten 1% reserves may function independently if well-spaced, perhaps even on a relatively small (e.g., 100-km perimeter) island such as Oahu, Hawaii.

For simplicity, SLOSS arguments generally ignore the interactive effects of refuge shape and size. However, habitat geometry (shape as well as size) importantly influences dispersal into and from a habitat, regardless of whether an organism's movements are home-ranging or free-ranging (Stamps et al., 1987). Edge "permeability" (i.e., whether a reserve is sited within a larger area of homogeneous "soft-edged" habitat or is a functional island surrounded by discontinuous "hard-edged" habitat) also significantly affects dispersal (Buechner, 1987; Stamps et al., 1987). Small increases in edge permeability have disproportionately large effects on dispersal when boundaries are hard, whereas habitat shape exerts a controlling influence on dispersal when boundaries are soft (Buechner, 1987; Stamps et al., 1987). For shoreline-bounded reef closures, the shape of the MFR is clearly more important to residential reef fishes if the MFR is sited within a larger region of similar habitat than if different habitats (e.g., extensive sand channels) are used to provide its physical boundaries.

### Future research

The overall net effect of the diverse compensatory and depensatory factors that may influence the movement patterns of fishes into and out of MFRs is beyond even semiquantitative appraisal at present. Major advances in our understanding of the function of MFRs await development of techniques that describe the fundamental transfer rates of fishes (Polacheck, 1990) and that further estimate the changes in movement rates that may occur as densities change over time. The results of my preliminary analyses suggest that future studies should focus on fast-growing, moderately vagile species such as many surgeonfishes, rather than reef transients or philopatriots. My preliminary conclusions should be reevaluated as more data become available for these and other types of reef fishes.

### Management potential

MFRs have the potential to enhance the biomass and spawning stock of species with rapid growth and moderate, fundamental transfer rates (Polacheck, 1990; the present paper). Many factors, however, contribute to whether this potential is likely to be realized in practice: the age schedule of harvest and the magnitude of fishing effort in the non-closed area; whether one versus a few or many MFRs of a given total area are used, thereby promoting progressively larger increases in fundamental transfer rates; and whether compensatory emigration acts to further inflate vulnerability and deflate $SSB/R$. Decisions as to the number versus size of MFRs that can be sited, given the total shoreline extent of reef available, are social issues. Size limits and fishing effort (bag limits) also are subject to their own management politics, and MFRs will not make them obsolete. Although the fast growth and moderate movement rates of certain tropical reef fishes predispose them to benefit from refuges, it is unlikely that the establishment of MFRs alone, without complementary regulation of effort and the size composition of catch in non-closed areas, can augment the SSB/R of fishes on heavily exploited island reefs.

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# Comparisons of spiny lobster *Panulirus marginatus* fecundity, egg size, and spawning frequency before and after exploitation

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**Abstract.** – Size-specific fecundities of spiny lobster *Panulirus marginatus* were compared for two time-periods: pre- and early exploitation or "before" (1978–81), and post-exploitation or "after" (1991). Fecundity was further evaluated within each time-period at two collection sites that represented the major lobster fishing grounds (Maro Reef and Necker Island) in the Northwestern Hawaiian Islands. Complementary data on egg size and spawning-frequency index were compared between study sites and time-periods.

Study sites and time-periods had no observable effects on egg size or spawning frequency, and there was no temporal effect on fecundity at Maro Reef. Fecundities at the two sites differed, however; "after" size-specific fecundity was an estimated 16±9% greater than "before" fecundity at Necker Island. Observations suggest that the recent increase in fecundity at Necker Island may reflect a compensatory (density-dependent) response to greater exploitation at this site. Results are discussed in terms of evidence for density-dependent responses in other, exploited spiny lobster stocks.

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The spiny lobster *Panulirus marginatus* (Quoy & Gaimard) is endemic to the Hawaiian Archipelago and Johnston Island (Brock 1973, Uchida et al. 1980). This species supported a major commercial fishery in the main Hawaiian Islands (MHI) prior to the rapid increases in demand after World War II (Uchida et al. 1980). Not until the expansion of the fishery into the Northwestern Hawaiian Islands (NWHI) began in 1977 did the species again support a valuable commercial enterprise, complemented with bycatches of slipper lobster *Scyllarides squamosus* (H. Milne-Edwards) and *S. haanii* (De Haan). A fishery management plan was created in 1983 to regulate the fishery based on minimum size limits and limited entry.

Prior to 1990, annual landings averaged 1–2 million spiny lobster worth US$4–6 million ex-vessel. Beginning in 1990 and continuing until the fishery closure in early 1991, however, landings fell heavily, equaling one-fifth of the long-term average (Landgraf 1991). These decreases reflected real declines in abundance, as both research and commercial catch per trap-haul (CPUE) similarly declined (Landgraf 1991). The present belief is that recent declines in the spiny lobster CPUE reflect a combination of continued, heavy exploitation and the occurrence of a series of poor year-classes, particularly at Maro Reef, one of the two major NWHI fishing grounds (Polovina 1991).

Recent research by Polovina (1989) has indicated that a density-dependent decrease in the size-at-onset of egg production occurred in NWHI spiny lobster from 1977 to 1986–87. Additional types of compensatory responses to lower population densities may be operative and may have a major influence on the dynamics of these lobster populations, but data are lacking (Polovina 1989). Included among these compensatory mechanisms is an increase in size-specific fecundity, a phenomenon suggested for other species of spiny lobsters (Chittleborough 1976 and 1979, Beyers & Goosen 1987, MacDiarmid 1989).

With the *a priori* prediction that size-specific fecundities might have increased for NWHI spiny lobster during the recent period of low population densities, we initiated a study of its fecundity and related reproductive life history. Prior to our study, little quantitative information existed on the fecundity of this species, and data were limited to the waters off Oahu in the MHI (Morris 1968, McGinnis 1972). Our objective is to compare the size-specific fecundities of NWHI spiny lobster between two time-periods: an early or pre-exploitation (hereafter referred to as "before") period in 1978–81, and a postexploitation ("after") period in 1991, when population densities had declined to a fraction of their pre-exploitation level.

## Methods and materials

### Specimen collection

Spiny lobster were collected using baited commercial traps at Maro Reef and on the offshore bank of Necker Island, the second of the two major NWHI fishing grounds (fig. 1, Polovina 1989). Lobsters were trapped during multiple cruises aboard chartered commercial vessels and the NOAA ship *Townsend Cromwell* during the summertime (May–August) breeding seasons of 1978–81 (the "before" period) and on a single cruise by the *Townsend Cromwell* during June–July 1991 ("after"). Commercial traps fished for a standard (overnight) soak period were used at each site during both time-periods. Specimens were similarly handled aboard the chartered vessels and the *Townsend Cromwell*.

### Sample processing

Lobsters were sexed, carapace length (CL) measured, and the egg developmental stage of egg-bearing ("berried") females scored as either Stage 1 (orange = freshly extruded), Stage 2 (brown = late development), or Stage 3 (white = hatching imminent). The CL, defined as the distance along the middorsal line from the transverse ridge between the supraorbital spines to the posterior margin of the carapace, was measured to the nearest 0.1 mm. Berried female specimens were either processed fresh in the ship's wet lab or flash-frozen (damp) aboard ship for processing ashore.

In the laboratory, brood sizes were estimated using Stage-1 females whenever possible so as to minimize the effect of potential egg loss (Morgan 1972, Annala & Bycroft 1987). The eight pleopods including egg clusters (setae bearing the egg masses) were separated by dissection and placed on absorbent paper towels. Egg clusters were then stripped off the pleopods onto preweighed weigh boats. Each individual female's total egg complement was weighed (damp weight to 0.1 mg) and then reweighed following determination of egg subsample weights; these two weighings were then averaged to provide a measure of the total egg mass. Random subsamples comprising a minimum (by weight) of 1% ($\bar{x}$=1.5%) of the female's total egg mass were weighed (0.1 mg) and later enumerated to estimate fecundity ($F_t$=total number of eggs) by proportion:

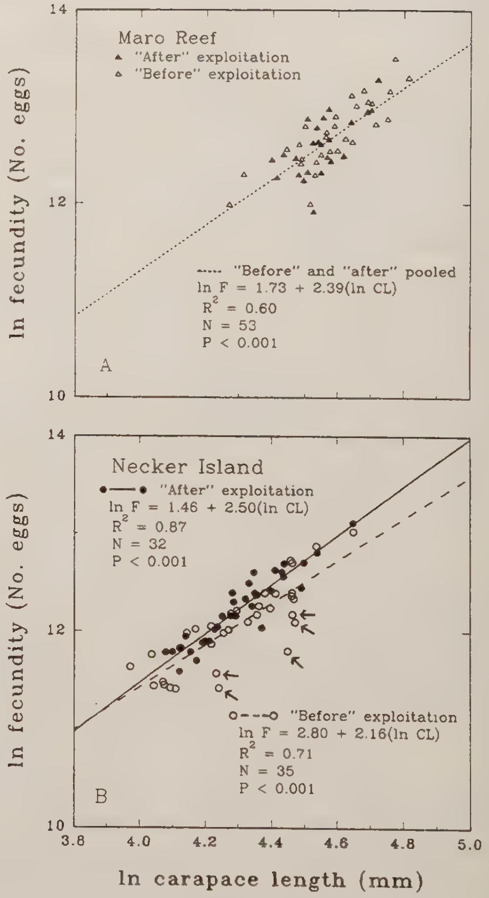

**Figure 1**

Scatterplots, least-squares regressions, and regression statistics for ln fecundity (number of eggs) versus ln carapace length (in mm) for berried female spiny lobster *Panulirus marginatus* trapped at two locations in the Northwestern Hawaiian Islands. **Maro Reef (top).** Data for the "before" (1978–81) and "after" (1991) periods are pooled for the regression analysis but plotted separately; one extreme outlier was omitted (see Results). **Necker Island (bottom).** Data for the "before" and "after" periods are plotted and analyzed separately. Arrows indicate the five most-extreme "before" data that were deleted in a re-analysis of the data (see Results).

$$F_t = F_s \cdot \left(\frac{W_t}{W_s}\right),$$

where $F_s$ = number of eggs in subsample, $W_s$ = weight of egg subsample, and $W_t$ = total weight of eggs. Some frozen-thawed egg masses were fixed in 4% formaldehyde for 1 month to harden eggs prior to weighing and counting. A single subsample was used to characterize the fecundity of each "before" specimen. Three replicate subsamples were used to estimate the sampling error of "after" fecundity determinations; the three pooled subsamples provided the best estimate of "after" fecundity. Total eggs were counted for one of the "after" specimens to gauge the accuracy of the weighing and counting procedures.

Egg sizes were estimated to complement the fecundity data. For a subset of both "before" and "after" Stage-1 specimens, a minimum of 25 eggs per female were randomly chosen and measured (random axis, at 50×) using a dissecting microscope with calibrated eyepiece micrometer.

Total egg production is the product of the number of eggs produced per spawning (brood size) and the number of spawnings. For females above threshold body sizes at onset of egg production at each of the sites during the two time-periods (Polovina 1989), we indexed spawning frequency based on the relative frequencies of berried (to total) females present in historical catch data of the Honolulu Laboratory. We used records of catches made at Maro Reef and Necker Island on summertime cruises during years within pre- and postexploitation periods when sufficient data were available (1977, 1988–91).

### Statistical analysis

Analysis of covariance (ANCOVA, SAS Proc GLM; SAS 1985) was used to compare mean fecundities between sampling periods; CL was used as a covariate to adjust for potential body-size differences between periods. As justified, central tendencies in fecundity were compared between periods ("before," "after") using least-square means (LSM) and their standard errors (SEM). Period and site (Maro Reef, Necker Island) were evaluated as class variables. Student's *t*-test, with degrees of freedom adjusted (as necessary) by Satterthwaite's approximation for unequal variances (Bailey 1981), was used to compare indices of spawning frequency between periods.

## Results

### Size-fecundity relationships

Paired CL and fecundity data were available for 54 spiny lobster from Maro Reef. At Necker Island, there were 67 analogous data pairs (Appendix A). Over 90% of the "before" specimens had Stage-1 eggs, and Stage-2 eggs were equally distributed among specimens from the two sites. Incidence of Stage-2 eggs appeared higher in the "after" samples from Maro Reef (8/24=33%) than in the analogous samples from Necker Island (3/32=10%). No lobsters with Stage-3 eggs were collected during either time-period. The coefficient of variation [$CV=(SD/\bar{x})\cdot 100$] of the triplicate "after" fecundity estimates was about 2%. The accuracy of the mean of the two weighings of an entire egg mass was within 4% of a total count.

At Maro, slopes were indistinguishable between periods, regardless of whether an obvious outlier (whose residual deviated 8.5% from its predicted value) was included (ln CL × period interaction: $F_{1,50}=0.06$, $P=0.81$) or was deleted from the analysis ($F_{1,49}\leq 0.01$, $P>0.99$). Slopes also were indistinguishable between the two periods at Necker Island ($F_{1,63}=1.17$, $P=0.28$).

Intercepts did not differ between periods at Maro Reef ($F_{1,50}=0.22$, $P=0.64$), but the period (intercept) effect at Necker Island was significant ($F_{1,64}=10.17$, $P=0.002$). Greater size-specific fecundity in the "after" period at Necker Island persisted, even if the five most-extreme "before" values (noted by the arrows in Fig. 1) were deleted and the analysis rerun ($F_{1,59}=4.40$, $P<0.05$). Using all available data, the power (1 minus Type-II error) of the test for period differences at Necker Island was 84%, for a critical Type-I error of 5% ($\alpha_2=0.05$).

CL significantly influenced fecundity at both Maro Reef ($F_{1,50}=70.6$, $P<0.001$; Fig. 1) and at Necker Island ($F_{1,64}=215.6$, $P<0.001$; Fig. 1). After adjustment for period differences in CL, the fecundity of lobsters at Necker Island was an estimated 16±9% greater during the "after" versus the "before" period (LSM±SEM of lnF = 12.224±0.034 and 12.072±0.033, respectively). Unlike the case at Necker Island, mean fecundity at Maro Reef differed only by <3% between the "before" and "after" periods (LSM±SEM = 12.680±0.041 and 12.651±0.046, respectively).

### Egg size

The median egg diameters of 22 females collected from Maro Reef and Necker Island during the "before" period were 0.58–0.69 mm. The analogous data for 53 "after" females were 0.61–0.73 mm, with a grand median of 0.66 mm.

Slopes of female body size/egg size (median diameter) relations were indistinguishable between sites (CL × site interaction: $F_{1,51}=0.55$, $P=0.46$). Intercepts also were indistinguishable: egg size was uninfluenced by site ($F_{1,52}=2.75$, $P=0.10$). Carapace length had no effect when sites were evaluated separately ($F_{1,52}$=0.11, $P$=0.75). However, female size significantly but weakly ($R^2$=0.08) affected egg size when data for the two sites were pooled (CL effect: $F_{1,53}$=2.104, $P$=0.04; median egg diameter = 30.2 EPU+0.039 $CL_{mm}$; $N$=55; EPU= 0.0197 mm).

### Spawning frequency

The relative frequency of berried/total adult females collected at Maro Reef and Necker Island during the summer of 1988 ($N$=3085 adult females), 1990 (1198), and 1991 (1165) was 0.246±3.401 ($\bar{x}$±1SD, $N$=6 site-year combinations). This index of the spawning frequency of females did not differ (t'=0.01, $P$>0.9) from 0.230±0.510, the estimated frequency for 3037 females collected during the summer of 1977 ($N$=2 site-years).

## Discussion

### Fecundity-body size relations

Exponents of the curvilinear, $F=a\cdot CL^b$, relations observed in this study ranged from 2.16±0.241 (statistically equal to 2.0) to 2.50±0.175 ($2.0<b<3.0$; Fig. 1). Perhaps both area of egg-bearing surface and volume (female body mass) influence fecundity in this species. Prior data on size-specific fecundity for an Oahu population of *P. marginatus* allow us to estimate the exponent in the equation $F=a\cdot CL^b$ as 2.96±0.31SE ($N$=11; table XV, Morris 1968).

A variety of linear:cubic relationships are available for other spiny lobster species. The following values of the exponent b in the power equation are either known or calculable for: *Panulirus interruptus* (1.0, Lindberg 1955), *P. homarus* (1.0, Berry 1971), *P. cygnus* (1.0, Morgan 1972); *Jasus verreauxi* (1.0, Kensler 1967), *J. edwardsii* (1.0, Kensler 1968; 3.01, McDiarmid 1989; 2.11–3.75, Annala & Bycroft 1987), *J. lalandii* (1.0, Beyers & Goosen 1987 and Pollock 1987; 3.58, Zoutendyk 1990), *J. tristani* (1.0, Pollock & Goosen 1991), *Nephrops norwegicus* (2.35, Thomas 1964 in Aiken & Waddy 1980). Best fits thus vary from linear to cubic both among species and among geographic populations within species. The only apparent pattern is the generally linear relationship between length and egg number in other *Panulirus* spp.

### Parameter interrelations

Although size-specific fecundity clearly changed between the "before" and "after" periods of exploitation for Necker Island lobster, neither egg size nor spawning frequency appeared to differ between the two sampling periods at either study site. Theoretically, size-specific fecundity might be expected to co-vary with egg size and spawning frequency (Gadgil and Bossert 1970). However, in many organisms, offspring size and number often do not track one another simultaneously or to an equivalent extent (Capinera 1979, Roff 1982). Therefore, our observation that egg size did not co-vary with egg number in *Panulirus marginatus* should not be surprising. Perhaps strong selection for planktonic larvae of relatively invariant body size is typical within particular populations of spiny lobster, even though average egg sizes might differ among populations of some species. This speculation is consistent with our observation that estimated egg volume varied only about 50% among female *P. marginatus* of a large range of body sizes from either site. This value is low compared with those of most marine teleosts (Bagenal 1971).

### Site and period comparisons

The site (geographic population) differences observed in this study of NWHI spiny lobster are not without precedent in other spiny lobsters. Annala & Bycroft (1987) and Beyers & Goosen (1987), for example, observed geographic differences in the size-specific fecundities of *Jasus edwardsii* and *J. lalandii*, respectively. For *J. edwardsii*, differences in size-specific fecundity were detected for populations ranging from extreme southern to northern New Zealand (Annala & Bycroft 1987). The spatial scale of the geographic pattern noted by Beyers & Goosen (1987) for *J. lalandii* was 600 km. Approximately 650 km separate Necker island and Maro Reef.

Unlike the Necker Island population, the fecundity of lobsters from Maro Reef was indistinguishable between the two sampling periods. The absence of a period effect at Maro Reef was not due to larger variance at a similar effect size (Cohen 1988); rather, the standard deviation of the residuals of lnF at Maro Reef (0.217) resembled that for Necker Island (0.206). There is the possibility, though, that size-specific fecundity has increased at Maro Reef too, but we were unable to detect it because of an artifact that particularly affected the fecundity estimates of "after" specimens from this site. Many of our "after" specimens from Maro Reef had Stage-2 eggs. Greater egg loss might have occurred during the handling of these specimens, because eggs at later stages of development may be more prone to dislodgement (Annala & Bycroft 1987). Anecdotal observations of the integrity of egg masses of the "after" females from Maro Reef suggest that, even though some additional egg loss might have occurred, it is unlikely to have been sufficient to obliterate an increase in size-specific fecundity of a magnitude similar to that observed for Necker Island lobster.

A significantly greater size-specific fecundity persisted at Necker Island in the "after" period even if the most-likely outliers from the "before" data were excluded from the analysis. This conservative re-analysis strongly suggests that period differences in the size-specific fecundities of Necker Island lobster are real. The magnitude of our best estimate of this difference (16%) further suggests that it represents a biologically meaningful change. A much more extensive series of before-and-after data would be necessary to resolve this issue beyond a reasonable doubt.

On balance, then, our data suggest that the size-specific fecundity of NWHI spiny lobster has increased at Necker Island, but likely not at Maro Reef, following a decade of heavy exploitation at both fishing grounds. Why and how can this be?

The data of Polovina (1989) suggest one possible explanation. The density-dependent decrease in mean carapace length-at-onset of egg production has been proportionately greater for female lobsters at Necker Island (10–15%, 67.8 to 57.9–60.8 mm) than at Maro Reef (6–9%, 74.8 to 68.2–70.5 mm; table 3, Polovina 1989). In 1977, the pre-exploitation densities (catch per trap-haul) of adult lobsters were higher at Necker Island ($\bar{x}$±SEM = 5.76±0.75) than at Maro Reef (3.89±0.45); yet by 1986–87, densities had declined more at Necker Island (to 2.14±1.24) than at Maro Reef (2.65±0.67; tables 1&2, Polovina 1989). By decreasing densities to a greater extent (thereby making more shelter or food resources available per lobster), it is possible that the effects of more intense cropping may now extend beyond decreased size-at-maturity to greater size-specific fecundity for Necker Island lobster.

Other factors besides exploitation might be somehow influencing the density and size-specific fecundity of *P. marginatus* at Maro Reef. Relatively few small lobsters were present at Maro Reef compared with Necker island during either of the time-periods used in our fecundity comparison (Polovina 1989; Fig. 1). Even so, disproportionately low recruitment at Maro Reef during 1986–88 might have recently exaggerated long-term baseline differences in the body-size distributions of exploitable *P. marginatus* at the two banks (Polovina & Mitchum 1992). Of the several possible reasons for higher pre-exploitation densities at Necker Island (more productive bottom habitat, fewer adult lobster predators), none is presently substantiated. Studies are in progress to evaluate the quality and distribution of bottom habitats among Maro Reef, Necker Island, and other NWHI lobster grounds.

### Density-dependent reproduction in lobsters

Density-dependent changes in egg production have been described or suggested for several other species of spiny lobster. Examples include changes in the number of spawnings (duration of spawning season) for individual females (Chittleborough 1976, 1979) as well as increases in size-specific fecundities (Thomas 1964, Beyers & Goosen 1987, MacDiarmid 1989) in response to lower population densities or otherwise greater food availabilities. Body size at onset of sexual maturity has responded in qualitatively different fashion to changes in lobster densities among different populations and species of lobsters. Several studies of *Jasus lalandii* (e.g., Pollock & Goosen 1991) have observed smaller body sizes at first maturation in stunted or physiologically stressed, high-density populations. As mentioned previously, Polovina (1989) has demonstrated the opposite response to reductions in adult densities resulting from exploitation. A fundamental, biological difference is whether size-at-maturity is an age- or size-dependent trait for a particular species and population. It is reasonable to expect species differences in the determination of maturation, and comparative studies of the mechanisms regulating the onset of maturation in different spiny lobsters would be informative.

### Statistical considerations

Several studies have evaluated, but been unable to detect, geographic variations in fecundity (Thomas 1964, Morgan 1972). The study by Morgan (1972) represents a case in which sample sizes were small and power was low despite nontrivial effect sizes. Future studies of lobster fecundity should report statistical power, especially when tests are unable to reject null hypotheses of no difference among populations.

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## Appendix A

Body size (carapace length, CL mm) and fecundity (F, no. eggs × $10^3$) data for individual spiny lobster *Panulirus marginatus* collected during "before" and "after" exploitation periods at Necker Island and Maro Reef. Data are ordered by increasing CL within period at each site.

| Maro Reef | | | | Necker Island | | | |
|---|---|---|---|---|---|---|---|
| Before | | After | | Before | | After | |
| CL | F | CL | F | CL | F | CL | F |
| 71.5 | 161 | 81.3 | 262 | 53.1 | 113 | 59.1 | 134 |
| 74.7 | 220 | 82.6 | 222 | 56.7 | 128 | 60.3 | 134 |
| 85.0 | 286 | 84.2 | 284 | 57.0 | 93 | 61.6 | 110 |
| 88.3 | 300 | 87.4 | 271 | 58.6 | 97 | 61.6 | 138 |
| 88.8 | 246 | 88.2 | 223 | 58.8 | 94 | 62.8 | 157 |
| 89.0 | 258 | 89.6 | 212 | 59.9 | 91 | 63.7 | 134 |
| 89.9 | 363 | 90.6 | 399 | 60.9 | 90 | 64.9 | 124 |
| 91.4 | 162 | 90.7 | 230 | 61.8 | 137 | 66.1 | 148 |
| 92.8 | 219 | 92.2 | 309 | 63.0 | 160 | 66.6 | 148 |
| 93.1 | 250 | 92.4 | 157 | 64.7 | 167 | 67.5 | 147 |
| 94.5 | 270 | 93.3 | 367 | 67.9 | 172 | 68.6 | 169 |
| 95.9 | 325 | 93.7 | 318 | 67.9 | 143 | 69.2 | 174 |
| 96.1 | 341 | 94.5 | 308 | 68.9 | 106[b] | 70.2 | 192 |
| 96.8 | 316 | 94.6 | 231 | 69.5 | 91[b] | 72.0 | 196 |
| 97.1 | 280 | 95.2 | 407 | 70.5 | 160 | 72.4 | 243 |
| 98.5 | 364 | 96.4 | 269 | 71.6 | 166 | 72.7 | 226 |
| 98.8 | 402 | 96.8 | 438 | 72.1 | 196 | 73.2 | 194 |
| 99.4 | 282 | 97.1 | 108[a] | 73.4 | 202 | 75.3 | 232 |
| 101.9 | 319 | 97.5 | 260 | 75.9 | 180 | 76.1 | 273 |
| 103.7 | 499 | 101.4 | 275 | 77.8 | 238 | 76.8 | 216 |
| 104.0 | 308 | 103.7 | 382 | 78.0 | 194 | 77.3 | 303 |
| 105.2 | 448 | 108.9 | 433 | 78.5 | 212 | 77.4 | 251 |
| 107.6 | 525 | 110.2 | 442 | 79.8 | 242 | 79.1 | 172 |
| 109.0 | 467 | 112.4 | 595 | 81.2 | 207 | 81.4 | 250 |
| 110.3 | 460 | | | 82.4 | 241 | 82.3 | 308 |
| 111.6 | 370 | | | 85.6 | 133[b] | 84.0 | 303 |
| 115.7 | 391 | | | 86.3 | 339 | 84.5 | 285 |
| 116.4 | 522 | | | 86.6 | 235 | 84.6 | 328 |
| 118.2 | 730 | | | 86.7 | 330 | 89.2 | 258 |
| 123.2 | 601 | | | 86.7 | 243 | 90.0 | 336 |
| | | | | 86.8 | 194[b] | 93.7 | 368 |
| | | | | 87.2 | 228 | 104.5 | 499 |
| | | | | 87.5 | 179[b] | | |
| | | | | 93.4 | 390 | | |
| | | | | 104.6 | 454 | | |

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[a] Extreme outlier deleted from final analysis.

[b] One of five most-extreme values deleted from conservative re-analysis (see Results).

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# Effects of dolphin group type, percent coverage, and fleet size on estimates of annual dolphin mortality derived from 1987 U.S. tuna-vessel observer data

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**Abstract.**–Amendments enacted in 1988 to the U.S. Marine Mammal Protection Act of 1972, coupled with changes during the 1980's in the composition of the international purse-seine fleet fishing "on dolphin" for yellowfin tuna in the eastern tropical Pacific (ETP), motivated a simulation experiment to assess the effects of fleet size and observer coverage level on estimates of cumulative annual mortality for dolphin stocks, where data quality differed greatly between stocks. Results from this simulation study provided a basis for subsequent U.S. legislation regarding criteria for comparing dolphin mortality rates of U.S. vs. non-U.S. fleets fishing in the ETP, pursuant to regulations governing import of tuna from this area.

Accuracy and precision of mortality estimates were influenced very strongly by data quality (dolphin group type) and moderately strongly by fleet size and level of observer coverage. Because neither fleet size nor dolphin group type can be controlled by a sampling program, desired levels of accuracy and precision in estimates of dolphin mortality can be achieved only by manipulating the level of observer coverage. The unexpectedly strong effect of dolphin group type implies that to protect all groups equally, observer levels should be chosen to accommodate the dolphin group type exhibiting the poorest-quality data.

U.S.-registered tuna purse-seiners in the eastern tropical Pacific Ocean (ETP) inadvertently kill dolphins during fishing operations (DeMaster et al., 1992). Since 1972 this kill has been monitored by scientific observers accompanying seiners on routine fishing trips. The kill data are monitored to determine whether annual quotas have been reached for dolphin mortality overall, and for several specific stocks of dolphins. If any quota is reached, fishing must cease on the affected stock for the remainder of the calendar year. Since 1989, the data have also been used to determine annual dolphin mortality rates for comparison with non-U.S. fisheries[1].

Prior to 1987, this kill monitoring was accomplished by observers on 30–50% of the trips made by U.S. purse-seiners during a given year. Thus, mortality was estimated rather than measured directly. In the absence of any alternative (i.e., higher rates of observer coverage), the accuracy and precision of these estimates were assumed to be adequate. This assumption was acceptable at the time because the U.S. fleet was large and generated many data. About 100 vessels fished the eastern tropical Pacific Ocean (ETP) each year, each vessel making two to five trips of about three-months duration each.

The situation changed dramatically in the 1980's when, for a variety of reasons (Sakagawa, 1991), the U.S. fleet began to decrease 20–30% per year, decreasing from over 90 vessels in 1981 to about 10 vessels in 1992. This decrease in size of the U.S. fleet was offset by a reciprocal increase in number of non-U.S. vessels fishing in the ETP. This increase has been dominated by Mexican vessels (fleet size exceeding 50 vessels by 1990) but also includes smaller fleets from several other nations. These smaller fleets range in size from 1 to about 20 vessels (IATTC Annual Reports, 1980–1991). In addition to these changes in composition of the international fleet, amendments passed in 1988 to the U.S. Marine Mammal Protection Act stipulated that yellowfin tuna caught in the ETP could be imported from non-U.S. countries only if mortality rates for those countries were comparable to U.S. kill rates.

These events created a strong incentive to evaluate the effects on mortality estimates of varying observer coverage levels and fleet sizes. Because the new regulations pertained to some individual stocks in addition to dolphin mortality overall, the previously uninvestigated effect of dolphin group type was also of interest.

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[1] The mortality estimator used in these simulations (kill/day) is not the same estimator used currently (1993) to determine mortality comparability (kill/set). The reasons for this appear in the methods section.

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The U.S. data set for 1987 provided a unique opportunity to investigate these effects. That year, for the first time, observers accompanied nearly 100% of trips by U.S.-registered purse-seiners to the ETP. By subsampling the 1987 data set, various observer levels and fleet sizes could be simulated and their effects on dolphin mortality estimates studied. In the absence of any other available data, these data were taken by NMFS as roughly representative of the international fleet. The simulation results guided subsequent legislation regarding mortality comparability criteria for non-U.S. fleets in the ETP.

Total annual mortality estimates are presented here for three dolphin groups (all stocks combined): spotted dolphin (*Stenella attenuata*); whitebelly spinner dolphin (*Stenella longirostris longirostris*); and common dolphin (*Delphinus delphis*). These three groups represent the range of data types (good, intermediate, and poor in quality) in the 1987 data set, and are generally representative of data types collected every year that may be affected by variable fleet sizes and levels of observer coverage in future fishing years.

Accuracy and precision of the mortality estimates are presented in terms of relative bias and coefficient of variation. Frequency distributions and analytic confidence intervals are examined for underlying patterns in mortality data responsible for generating observed patterns in accuracy and precision.

## Methods

### Data

During 1987, 34 U.S.-registered purse-seine vessels carrying certificates that permitted fishing "on dolphins" made a total of 134 fishing trips to the eastern tropical Pacific Ocean (ETP). Of these vessels, 33 made 124 trips that were observed by either a National Marine Fisheries (NMFS) or an Inter-American Tropical Tuna Commission (IATTC) technician. These 124 observed trips comprised the entire population of trips for this study. They accounted for 93% of all trips and 96% of all days spent at sea in the ETP by U.S.-registered tuna purse-seiners during 1987. Trips made by individual vessels within fleets were considered replicates and observed trips were assumed to represent unobserved trips accurately. Data consisted of records of date, time, trip number, set number, and kill per set.

Between 4 and 20 vessels carrying observers departed each month during 1987 (Fig. 1). Approximately the same number (although not necessarily the same vessels) of observed vessels (about 30) fished in the ETP during any given month (Fig. 2). Just over half the trips (65/120) lasted about three months. Trip duration ranged from one to six months (Fig. 2). Number of trips incurring mortality of each dolphin group type ranged from 93 (offshore spotted dolphins; Fig. 3) to 12 (common dolphins).

Dolphin mortality data were not stratified geographically, despite the demonstrated efficiency of this stratification scheme (e.g., Hall and Boyer, 1986) because it can be applied only when data sets provide reasonable numbers of reasonably homogeneous data per stratum. Data tend to be so variable for the less frequently killed groups, such as common dolphins, that mortality estimates tend to be very imprecise (and infrequent) even without stratifying data. This is likely to be a problem for all dolphin types for small fleets in every year[2].

Data quality differed between group types in both frequency and extent of kill. Data for offshore spotted dolphins were the "best" in terms of being most plentiful and most evenly distributed between trips collecting data. The frequency distribution of kill per day per trip (i.e., number of dolphins killed per number of days at sea, for a given trip) is relatively smooth (Fig. 3). Most trips killed about 0.5 dolphins per day, a few

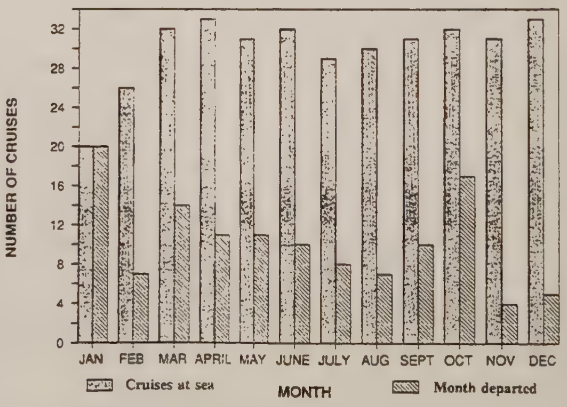

Figure 1
Number of observed U.S.-registered tuna purse-seine vessels at sea, and number of observed vessels leaving port each month during 1987.

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[2] At the time this study was conducted (1988–1989), there were no legal requirements for data stratification. Subsequent to this study, the U.S. Congress enacted legislation (Federal Register Notice Vol. 54, #43, Tuesday March 7, 1989; 54 FR9438-9451) requiring stratification of data for annual mortality estimates into three geographic strata and two dolphin groupings (common dolphins, and all other dolphins).

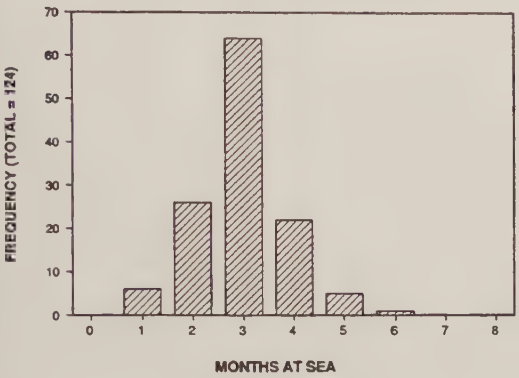

**Figure 2**
Months spent at sea per trip by U.S.-registered tuna purse-seine vessels carrying observers during 1987.

trips killed no spotted dolphins, and trips with higher kills occurred with decreasing frequency. Data for whitebelly spinner dolphins were intermediate in quality. They were fewer but still relatively smoothly distributed. About half the trips killed no whitebelly spinner dolphins, but of those incurring mortality, most trips were responsible for about 0.1 dolphins per day. Higher kills again occurred with decreasing frequency, with little evidence of extreme outliers. Data for common dolphins exhibited the worst quality, being both sparse and very unevenly distributed. Of the 12 trips incurring mortality of common dolphins, 9 killed about 0.5 dolphins per day, 2 trips killed 1–1.5 dolphins per day, while the remaining trip was responsible for about 9 deaths per day. That one trip was responsible for 67% (594/882) of U.S.-caused common dolphin deaths during 1987.

## Simulations

We first selected randomly and without replacement 5, 10, or 20 vessels from the total of 33 observed vessels (Fig. 4). We then sampled randomly and without replacement, 25%, 50%, or 75% of the trips made by each of these selected vessels, without regard to actual timing of those trips throughout the year. We did not force temporal stratification on these small fleet simulations because fleet sizes of 5 or 10 vessels generated so few data.

Vessel selections were replicated 10 times at each combination of fleet size and percent coverage. Trip selections were replicated 50 times from each of the 10 sets of selected vessels. Thus, selected vessels were the same within each set of 50 replicate samples of trips but differed between sets of 50 replicates. Trips conducted by selected vessels in each sample fleet represent the "population" of trips for that fleet replicate.

Each set of 50 replicate selections of trips from a given set of selected vessels generated 50 estimates of cumulative annual mortality (cumulative mortality through December 31). For each set of 50 estimates, we calculated the mean estimate, the coefficient of variation for the mean estimate, and the relative bias of the mean estimate. Thus for each combination of fleet size and percent coverage we generated 10 averaged estimates of annual mortality, 10 coefficients of variation, and 10 estimates of relative bias.

Because the "true" kill varied between fleet replicates depending on the particular vessels and trips selected, the average of these 10 averaged estimates (from the 50 replicates) of annual mortality is not a particularly useful measure in this study. This average represents only the average of the 10 sets of vessels that happened to be chosen for the 10 replicates of fleet size. However, the coefficients of variation and estimates of relative bias for each of the 10 averaged estimates *are* relevant indicators of the ability of the estimation process to precisely or accurately, or both, reflect the true kill, whatever it happens to be for a particular sample of vessels. Accordingly, we present results only for the averages of the 10 estimates of CV and RB generated for each combination of percent coverage, fleet size, and dolphin mortality type. We do not discuss directly the individual mortality estimates.

## Estimates

The estimates in this simulation study were derived by using the ratio estimator kill per day, rather than the more precise estimator kill per set (Lo et al., 1982; Hall and Boyer, 1986) because at the time this study was designed and executed, kill per day was still the estimator of choice for NMFS[3].

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[3] Kill/day was used by NMFS up until 1987 when 100% observer coverage began, because the quota system required that dolphin kills be monitored continuously throughout the year rather than simply summed at the end of the year. Estimates based on kill/day can be made on a reasonably real-time basis because the day that a vessel leaves port is a readily available datum, and observers report kills by radio on a biweekly basis throughout each observed trip. Number of days fished by the entire fleet (observed plus unobserved) can then be determined relatively simply by summing the number of days at sea since leaving port, and total kill estimated as the product of total fleet days times the estimator kill/day. Biweekly estimates based on kill/set are not possible because observers are not permitted to report set data over the radio. Set data do not become available until after vessels have returned to port.

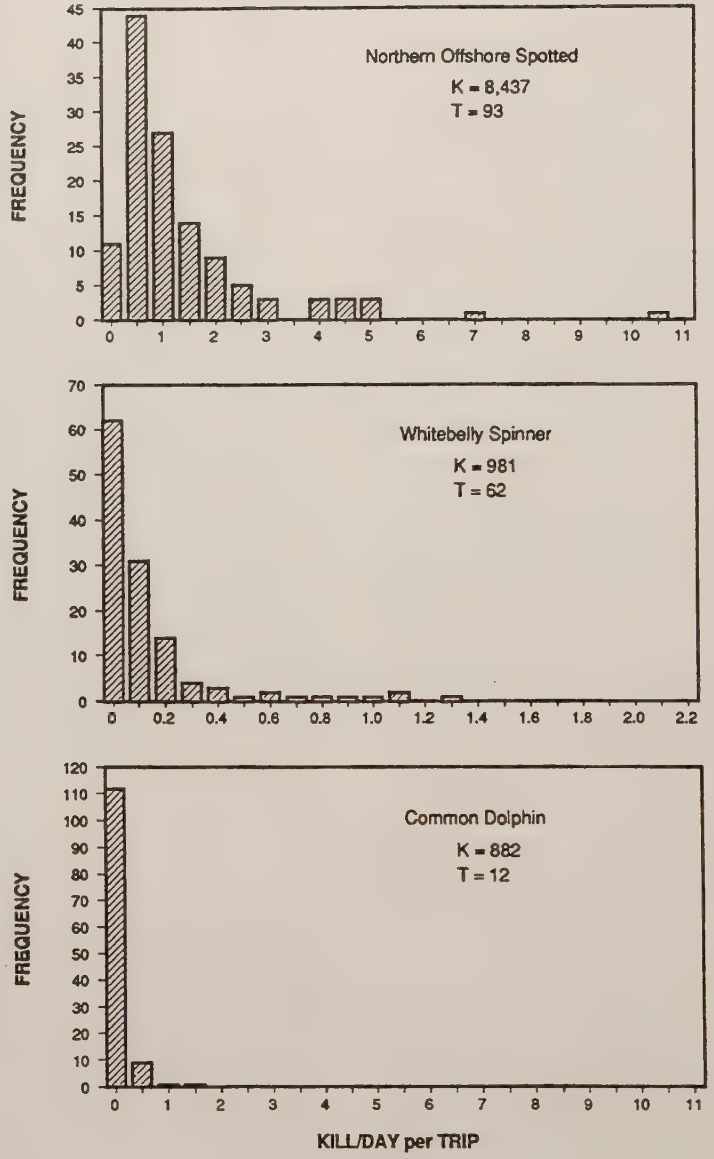

**Figure 3**

Kill per day during observed trips (124 trips total) by 33 U.S.-registered tuna purse-seiners fishing in the ETP during 1987, for three species of dolphins representing the range of mortality data types. Scales of ordinates and abscissas differ between panels. *K* is total observed kill during 1987; *T* is number of trips incurring kill.

Factors and levels included dolphin group$_i$ ($i$=1,2,3; offshore spotted, whitebelly spinner, and common dolphin), fleet size$_j$ ($j$ = 1,2,3,4; for 5, 10, 20, or 33 boats), fleet replicate$_k$ ($k$=1,..,10), percent coverage$_l$ ($l$=1,2,3; for 25%, 50%, and 75%) and percent coverage replicate$_m$ ($m$=1,...,50).

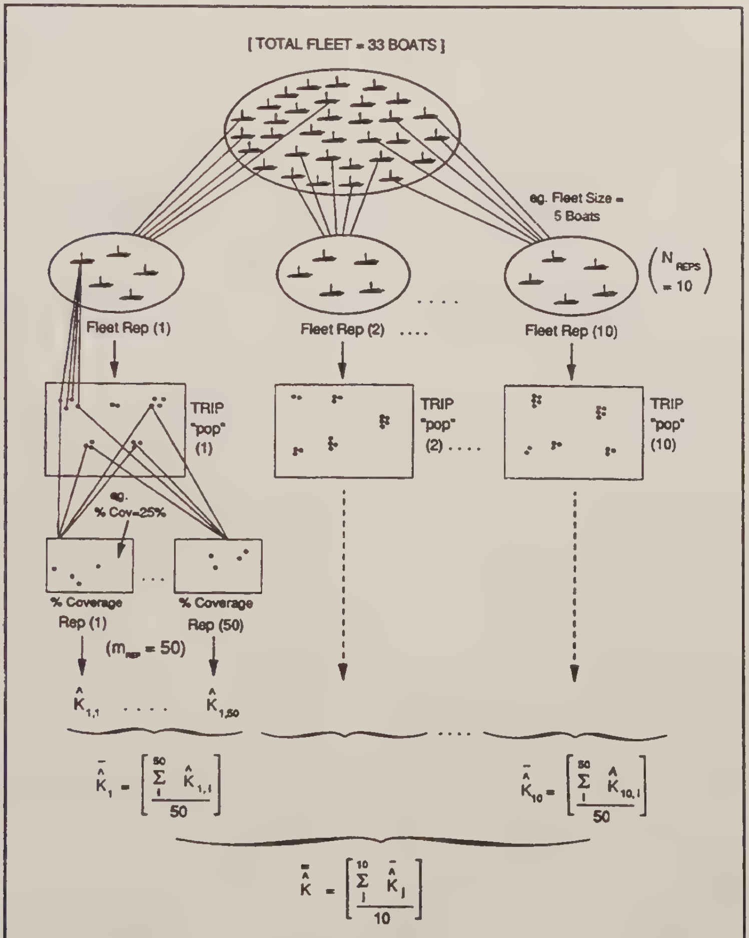
[TOTAL FLEET = 33 BOATS]
eg. Fleet Size = 5 Boats
$\left(\begin{matrix}N_{REPS}\\=10\end{matrix}\right)$
Fleet Rep (1)
Fleet Rep (2) ....
Fleet Rep (10)
TRIP "pop" (1)
TRIP "pop" (2) ....
TRIP "pop" (10)
eg. % Cov=25%
% Coverage Rep (1)
% Coverage Rep (50)
$(m_{rep} = 50)$
$\hat{K}_{1,1}$ .... $\hat{K}_{1,50}$
$\bar{\hat{K}}_1 = \left[\frac{\sum_{i}^{50} \hat{K}_{1,i}}{50}\right]$
$\bar{\hat{K}}_{10} = \left[\frac{\sum_{i}^{50} \hat{K}_{10,i}}{50}\right]$
$\bar{\bar{\hat{K}}} = \left[\frac{\sum_{j}^{10} \bar{\hat{K}}_j}{10}\right]$

**Figure 4**
Sampling procedure for simulation study.

Within each replicate, cumulative annual mortality for a given group of dolphins (*YHAT*) is estimated as

$$YHAT_{ijklm} = (K_{ijklm} / DAYS_{jklm}) * TFDAYS_{jk}$$

where $K_{ijklm}$ is the observed cumulative annual kill on all selected trips, $DAYS_{jklm}$ is the observed number of days, and *TFDAYS* is the total number of days spent at sea by all vessels selected for that replicate.

For each set of 50 replicate estimates of annual mortality for a given fleet size, percent coverage, and dolphin group type, we calculated the average estimate ($YAVE_{50}$), the relative bias of that estimate ($RBY_{50}$), and the coefficient of variation of that estimate ($CVY_{50}$) as follows

$$YAVE_{50ijkl} = (1/50) * \sum_{m=1}^{50} YHAT_{ijklm}$$

$$RBY_{50ijkl} = 100 * (YAVE_{50ijkl} - known\ kill_{ijk})/known\ kill_{ijk}$$

and

$$CVY_{50ijkl} = [\sqrt{MSE(YAVE_{50ijkl})}/known\ kill_{ijk}]*100$$

where

$$MSE(YAVE_{50ijkl}) = \sum_{m=1}^{50}(YHAT_{ijklm} - known\ kill_{ijk})^2$$

and

$$BYAVE_{50ijkl} = YAVE_{50ijkl} - known\ kill_{ijk},$$

where $BYAVE_{50ijkl}$ is the bias of $YAVE_{50}$, and $V(YAVE_{50ijkl})$ is the variance of $YAVE_{50ijkl}$, calculated as

$$V(YAVE_{50ijkl}) = (1/49) * \sum_{m=1}^{50}(YHAT_{ijklm} - YAVE_{ijkl})^2$$

(Cochran, 1977).

The preceding equations produce 10 $YAVE_{50}$'s, 10 $RBY_{50}$'s, and 10 $CVY_{50}$'s for each combination of fleet size, percent coverage, and dolphin group type.

The average of these 10 $RBY_{50}$'s is

$$RBY_{10ijk} = (1/10) * \sum_{k=1}^{10} (RBY_{50ijkl}),$$

and the average of the 10 $CVY_{50}$'s is

$$CVY_{10ijk} = (1/10) * \sum_{k=1}^{10} CVY_{50ijkl}.$$

### Sampling distributions and confidence intervals

To facilitate interpretation of patterns seen in relative bias and coefficients of variations, we plotted both frequency distributions and analytic 95% confidence intervals for an arbitrarily selected single set of 50 individual replicate estimates of mortality derived under various combinations of conditions. The frequency distributions and confidence intervals illustrate, in particular, variations due to differences between replicates in the fleet selected, in contrast to the relative bias and coefficient of variation, which pertain to sampling properties of the estimator. Only one set of 50 replicates, of the 10 sets generated under each combination of fleet size and coverage level, is illustrated for each combination because the general messages conveyed by the figures were the same for all sets.

Frequency distributions and confidence intervals are plotted only for the cases of 5 and 20 boats at 25% and 75% coverage. Combinations of these values spanned the range of fleet sizes investigated and enabled us to examine whether problems might occur even with coverage as high as 75% when fleet size is as small as 20 (or worse, 5) boats.

The frequency distributions of the 50 estimates illustrate graphically the influence of various combinations of fleet size and observer coverage level on the behavior (dispersion) of the estimator itself (kill/day). The analytic confidence intervals for the 50 estimates illustrate the influence of various combinations of fleet size and observer coverage level, on the estimated precision that may be associated with any individual estimate.

The analytic confidence intervals for individual replicate estimates of mortality were calculated by the International Mathematical and Statistical Library (IMSL) routine SMPRR for ratio estimates (IMSL, 1987). This routine calculates confidence intervals for ratio estimates using the analytic formula for approximate variance of a ratio. The procedure is based on the assumption that a normal approximation to the ratio variance is appropriate (Cochran, 1977; IMSL, 1987). Where data are sparse (fewer than 30 data points in the data set; i.e., in most of the cases in these simulations) this assumption is generally inappropriate (e.g., Cochran, 1977), but for single replicates we had no computationally simple alternative. Bootstrapping confidence intervals for these individual replicates would have eliminated any need for a normal approximation but would have required significantly more computer time to convey essentially the same gross patterns and general message.

## Results

### Relative bias (RB)

RB was generally small overall, but exceeded the management objective of 5% for common dolphins and whitebelly spinner dolphins when coverage was low (25%; Fig. 5).

### Coefficients of variation (CV)

CV decreased with increasing percent coverage and with increasing fleet size in both the "best" data group (offshore spotted dolphin; Fig. 6) and in the "intermediate" data group (whitebelly spinner dolphin). CV decreased with increasing percent coverage but showed no consistent effect of fleet size in the "worst" data group (common dolphin).

### Sampling distributions

Frequency distributions were affected somewhat by fleet size (primarily by shifting the central tendency), noticeably by percent coverage (primarily by decreasing the spread of the distribution), and very strongly by dolphin group type (primarily in terms of the number of modes in the distributions; Figs. 7, 8, and 9). Bias and variability increased with small sample sizes and non-smooth data distributions.

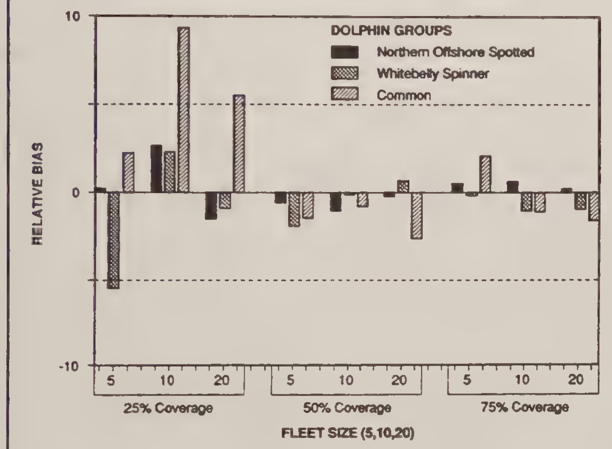

**Figure 5**

Average relative bias (%) in estimates of annual dolphin mortality as a function of fleet size and percent observer coverage. Dashed line at +5% and −5% indicates management target.

Distributions of mortality estimates for offshore spotted dolphins tended to be relatively narrow and unimodal for fleets of both 5 and 20 vessels, at high coverage (75%; Fig. 7). Distributions remained unimodel but were more dispersed, at low coverage (25%). Distributions for whitebelly spinner dolphins were also unimodal in general but tended to be more dispersed than was the case for offshore spotted dolphins (Fig. 8). Distributions for common dolphins were markedly bimodal and dispersed under all sampling conditions, reflecting the selection (or not) of the one trip with unusually high kill (Fig. 9).

Modal values of mortality estimates for all three dolphin types increased with increasing fleet size (not surprisingly, because more boats generally kill more dolphins) regardless of coverage level. Dispersion also increased with fleet size, more obviously when observer coverage was low than when coverage was high, as more data became available for analysis.

## Confidence limits

Confidence limits were affected similarly to frequency distributions. Limits were affected most strongly by dolphin group type, very noticeably by percent coverage, and less strongly but still noticeably by fleet size (Figs. 10, 11, and 12).

Mortality estimates were most stable and confidence intervals dramatically reduced for offshore spotted dolphins at high (75%) observer coverage (Fig. 10). Mortality estimates were more variable and confidence intervals wide and ragged, even with a relatively large fleet (20 boats), for offshore spotted dolphins at low observer coverage (5%). Intervals were most unstable at the combination of lowest observer coverage and smallest fleet size[4]. Confidence interval patterns for whitebelly spinner dolphins were intermediate, being more variable than patterns for northern offshore spotted dophins but being less variable than patterns for common dolphins (Fig. 11). At low coverage and small fleet size, confidence intervals for whitebelly spinner dophins showed the same bimodality characteristic of confidence intervals for common dolphins under all conditions. At high coverage, confidence intervals showed the same relatively stable and

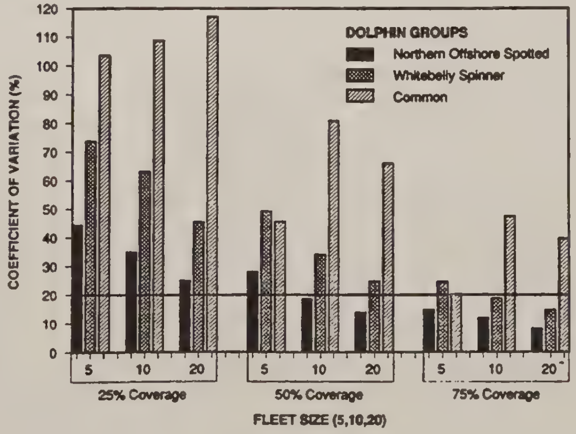

**Figure 6**

Coefficient of variation (percent) in estimates of annual dolphin mortality as a function of fleet size and percent observer coverage. Dark horizontal bar at 20% indicates management target.

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[4] The irregular pattern of the confidence intervals observed for mortality estimates from small fleets (e.g., 5 boats) with low coverage (e.g., 5 boats, 25% coverage) are not surprising because this combination of fleet size and percent coverage means that the mortality estimates are being derived from about 4 observed trips during an entire year (assuming 5 boats make 3 trips/year, 15 trips × 0.25 = 4 trips).

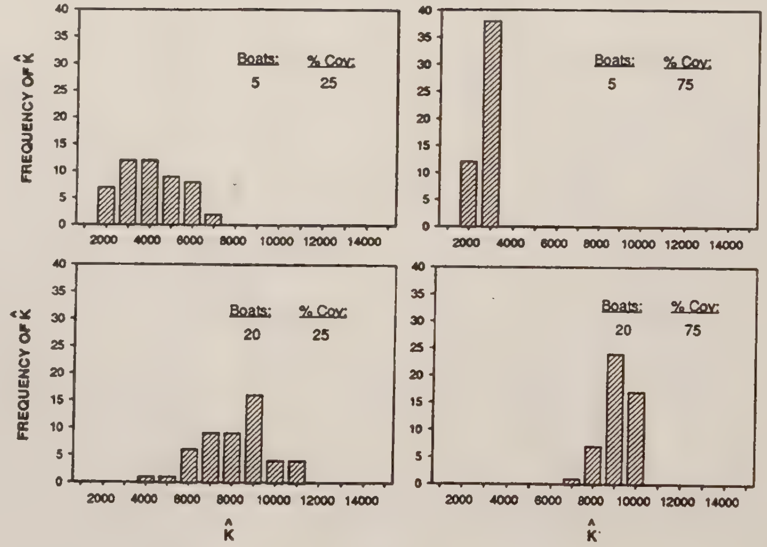

**Figure 7**

Effect of percent coverage and fleet size on frequency distributions of annual mortality estimates for **offshore spotted dolphins**, from one set of 50 replicates.

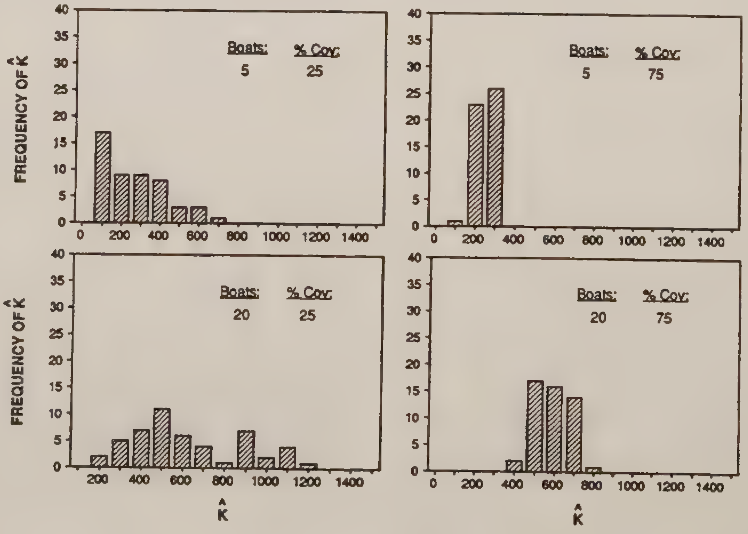

**Figure 8**

Effect of percent coverage and fleet size on frequency distributions of annual mortality estimates for **whitebelly spinner dolphins**, from one set of 50 replicates.

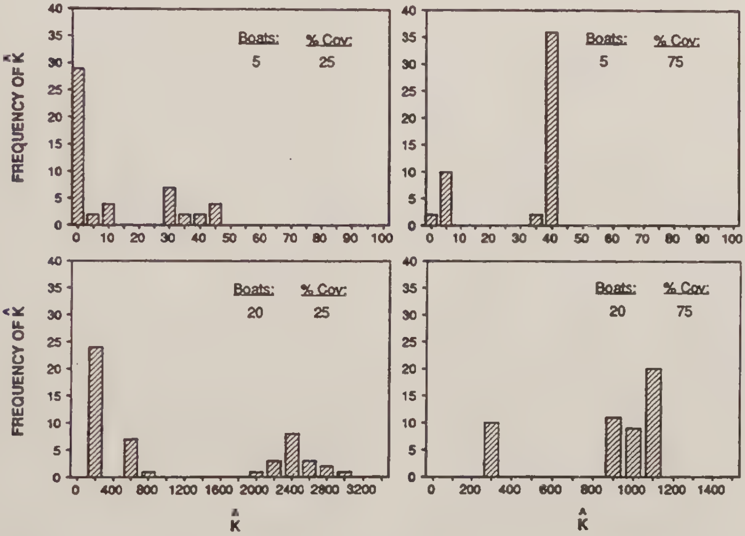

**Figure 9**

Effect of percent coverage and fleet size on frequency distributions of annual mortality estimates for **common dolphins**, from one set of 50 replicates.

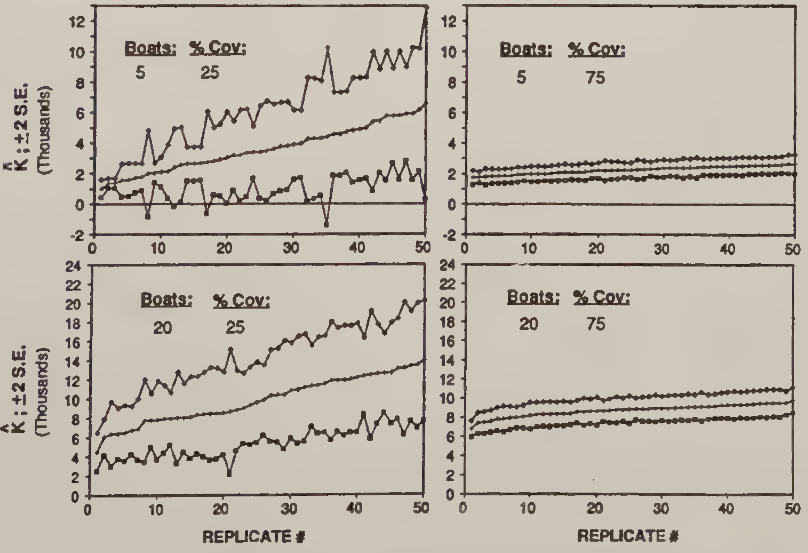

**Figure 10**

Effect of percent coverage and fleet size on analytic confidence intervals of replicate annual mortality estimates for **offshore spotted dolphins**. Replicate estimates sorted by estimate level, from one set of 50 replicates. Note differences between panels in Y scale.

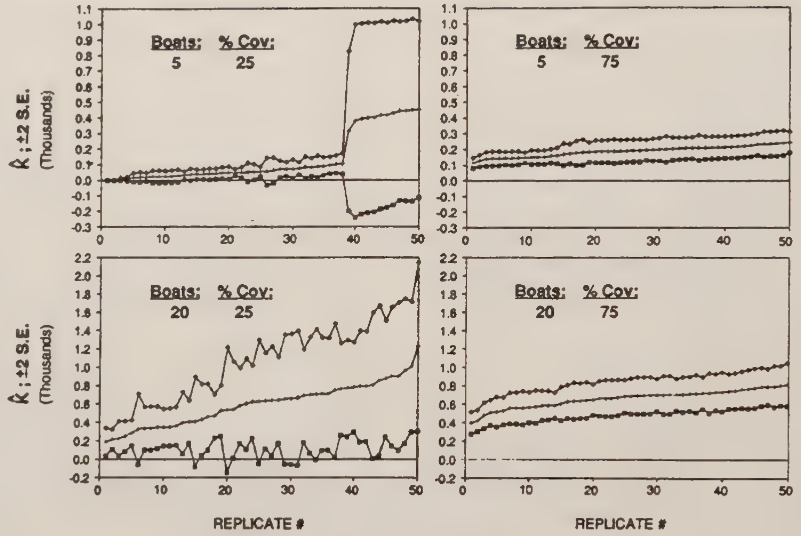

Figure 11

Effect of percent coverage and fleet size on analytic confidence intervals of replicate annual mortality estimates for **whitebelly spinner dolphins**. Replicate estimates sorted by estimate level, from one set of 50 replicates. Mortality estimates expressed in thousands. Note differences between panels in Y scale.

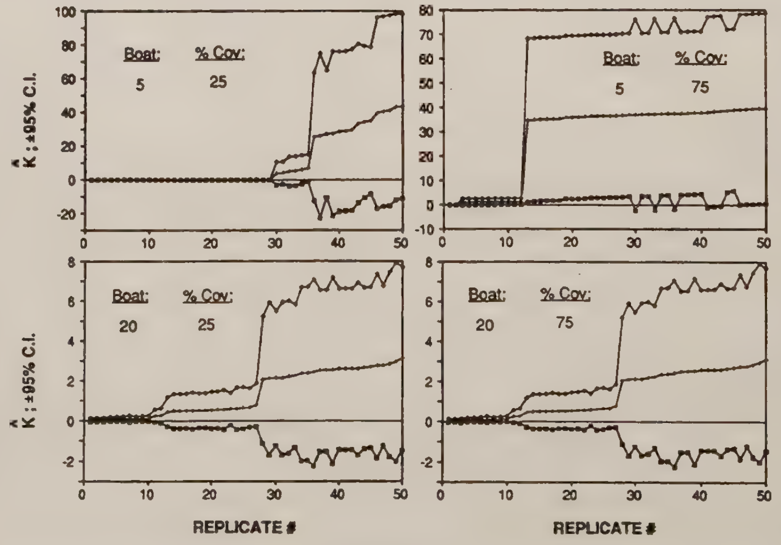

Figure 12

Effect of percent coverage and fleet size on analytic confidence intervals of replicate annual mortality estimates for **common dolphins**. Replicate estimates sorted by estimate level, from one set of 50 replicates. Mortality estimates expressed in thousands. Note differences between panels in Y scale.

narrow limits seen for offshore northern spotted dolphins at high coverage. Confidence intervals for common dolphins illustrate the problems inherent in relatively heterogeneous data, where mortality is sometimes quite high, usually relatively low, and data overall are relatively few. For this species, confidence intervals were extremely variable even with relatively high coverage (Fig. 12) and were very narrow (or nonexistent) for replicates which fortuitously included only low-kill data, but very wide for replicates including a few very high kills.

Although these analytic confidence intervals are clearly inappropriate measures for precise estimation of variance characteristics of the estimates (note negative intervals in some cases; Figs. 10, 11, and 12), they are presented here because they provide an effective illustration of the effects of varying conditions on the variability of the mortality estimates. Despite the inter-group differences, the general response to increasing coverage and increasing fleet size is similar in all three dolphin group types. Confidence intervals become narrower and more stable as more data become available.

## Discussion

### Dolphin group type

Of the three factors investigated here (dolphin group type, observer coverage level, and fleet size), dolphin group type had the greatest effect on dolphin mortality estimates, followed by percent coverage and fleet size. This hierarchy of effects is controlled by two characteristics of the kill data for each dolphin group type—*frequency* (the number of times that mortality occurs) and *variability* (differences between times in the number of dolphins killed). The *total* number killed can have relatively little influence on the quality of the estimate. This is illustrated by comparing results for whitebelly spinner dolphin and common dolphin. Although total kill was comparable for both dolphin group types (981 deaths of whitebelly spinner dolphin, 882 deaths of common dolphin; Fig. 3) the data sets differed markedly both in number of trips incurring kill (62 for whitebelly spinner dolphin, 12 for common dolphin) and in the distribution of kill per day among those trips (Fig. 3).

The data set for common dolphins exhibits the worst of both characteristics; frequency of kill was low (few trips killed common dolphins) and variability between trips in kill per day was high. These problems exemplify an unfortunate interaction between data collection problems and the ecology of the dolphins themselves. Mortality of common dolphins due to the U.S. fleet during 1987 was *infrequent* because the geographic range of this species is relatively limited and occurs primarily within Mexico's Exclusive Economic Zone. U.S. vessels rarely fish in this area, therefore common dolphins rarely die in U.S. tuna nets in this area. Mortality was *variable* at least in part because common dolphins have an unfortunate habit (in this context) of forming very large schools, pre-disposing them to the possibility of very large-kill "disaster" sets.

The data set for whitebelly spinner dolphin exhibits a problem with only one of the characteristics; data are relatively infrequent. Unlike the case for common dolphins, kill per day was not extremely variable. This similarity in kill per day generates statistics for whitebelly spinner dolphin that are much less biased and variable than for common dolphin.

### Observer coverage level

The effect of observer coverage level is influenced both by fleet size and dolphin group type. To achieve a desired level of precision and accuracy in mortality estimates, observer coverage levels will have to be higher in smaller fleets because the available data will be fewer, and higher in dolphin groups with "messy" data, because observer coverage levels affect the probability of encountering an unusually large kill[5].

Observer coverage will need to be relatively high even for large fleets, when estimating mortality of dolphins with sparse and heterogeneous data. For example, with kill data as sparse and variable as was the case for common dolphins in 1987, nearly 100% coverage would be required to generate CV's lower than 20% regardless of fleet size (Fig. 6). With more frequent and less variable kill data, such as for northern spotted dolphin in 1987, CV's lower than 20% can be achieved with 50% coverage of 10-boat fleets (Fig. 6). When fleet size drops to 5 boats, even this relatively well-behaved data set requires coverage at about 75% to achieve CV's less than about 20%. With coverage as low as 25%, even a fleet size of 20 boats was insufficient to meet the management objective of 20% CV.

### Fleet size

In smaller fleets, each data point comprises a larger fraction of the available mortality data. In particular, the influence of unusually large mortalities (e.g., the one trip responsible for over 500 deaths of common dolphins) will be much greater in smaller fleets.

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[5] The possibility of high kills is more important than the possibility of low kills; this is because all dolphin group types experience zero kill frequently (therefore it is not unusual or unexpected). Also, zero kill is a definitive lower bound, while the upper bound on kill is limited only by the potential school size of the dolphin group.

The accuracy and precision of mortality estimates are affected less by fleet size *per se* than by observer coverage level for a given fleet size, and the fleet's variability in kill per day. Kill per day is affected not only by the fishermen's choices of fishing methods and areas, but also by the type of dolphin found associated with a given school of tuna. Because these are not factors that can be controlled, small fleets will generally require higher coverage level than larger fleets to achieve a given level of accuracy and precision in mortality estimates.

### Simulation procedures and estimates

The simulation procedure used in this study was designed to reflect the sampling process as it would occur in the real world. More precise and less biased estimates of mortality rates for the population of trips contained in the 1987 data set would have resulted from simple random sampling of the 124 trips in the data set as a whole. But simple random sampling implicitly assumes that all vessels are equal in fishing ability. This is not the case, and it is likely that some fleets as a whole may have greater (e.g., those newer to purse-seining and therefore less experienced) or lesser (e.g,, the more experienced fleets) mortality rates than the average for the ETP purse-seine fleet overall. In addition, in the real world, not all trips made by all purse-seine vessels fishing in the ETP would be available for sampling. Only trips made by the vessels in a particular fleet would be available for sampling, and only those vessels actually observed would contribute data. If vessels (or more properly, the crew) differ in their ability to release dolphins unharmed (or not), then fleets with more (or fewer) "low kill" vessels will have lower (or higher) mortality rates than other fleets of comparable size. Although it would have been possible to estimate the number of trips that would have been made, on average, by a fleet of a given size, and to have then randomly sampled that many trips from the 1987 data base, the results would have been unrealistically precise. The cluster sampling resulting from the selection of trips only after selecting vessels adds variability in the estimates but is more realistic than simple random sampling. The sampling scheme used here is a single stage cluster sampling, for which a ratio estimator is the most appropriate choice of estimation procedure (Cochran, 1977).

## Discussion

Although the kill-per-day estimator used in this simulation study is no longer used by NMFS because 100% observer coverage has made estimation unnecessary, the results of this study have general implications for current estimation procedures based on kill per set (e.g., Hall and Boyer, 1986) and for mortality estimation procedures in general where data quality may vary between stocks.

The uneven structure of the data set for common dolphins has unfortunate implications for deriving estimates of mortality for dolphin groups that are characterized by having such infrequent and widely variable kill per day. Specifically, estimates of mortality can vary widely depending on which trips happen to be chosen. In our simulation, we could resample the total population of vessels repeatedly, thus generating relatively unbiased, though individually variable, estimates of mortality. In the real world, only one sample (one set of mortality data per dolphin group type) will be collected per year. If this sample is collected under low percent coverage, it appears very likely that the data may be affected by undetectable sampling biases. This bias is more likely to underestimate than to overestimate mortality because sets with large kill are rare and likely to be underestimated, even though the mortality during such sets may be responsible for a disproportionately large percentage of the total kill.

The problem with missing the rare large-kill sets is that the kill in these sets can apparently be one or two orders of magnitude greater than the "usual" kill. For very abundant groups, missing a few large kills will miss only a small percentage of the total number of dolphins in the group; underestimating mortality could be relatively harmless. For less abundant groups, the large kills might represent a significant proportion of the existing stock. Underestimating this mortality could lead to seriously underestimating the impact of mortality due to fishing operations on these stocks.

In the case of the 1987 data set for dolphin kill by the U.S. fleet, coverage greater than 96% (the highest observed) would be required for all boats in order to generate mortality estimates for common dolphin with CV's less than 20%. Alternatively, if only the most abundant groups are considered (e.g., offshore spotted dolphin), CV's less than 20% could be achieved with only 50% coverage of fleets as small as 5 boats. There appears to be no unique solution that is optimal for all groups.

In addition, the poor quality of the data presented here for common dolphin in fact underestimates the true extent of the problem for this species. In actual practice, the species is managed as three separate stocks rather than as one combined stock as presented here. The data are thus extremely sparse for the individual stocks, and the problems with estimating mortality, given anything less than full observer coverage, are greatly exacerbated.

The results of these simulations, in particular the results for five-boat fleets, and common dolphins, strongly influenced subsequent regulations related to comparability criteria for import of tuna caught by non-U.S. fleets. These regulations now require that mortality data for common dolphins be stratified separately from all other stocks, and that non-U.S. fleets meet the U.S. requirement for 100% observer coverage[6].

Of the three factors discussed here (dolphin group type, percent coverage, and fleet size), only percent coverage can be controlled by the sampling program. Our results imply that providing maximum protection for all dolphin groups would require mandating coverage to achieve a desired level of statistical precision for the dolphin group type with the least statistically stable data.

## Acknowledgments

The U.S. fleet simulation study was designed by Bruce Wahlen. Nancy Lo and Peter Perkins provided insightful advice about sampling procedures and statistical methods. We thank also the participants in the Workshop on Estimating Dolphin Mortality, and two anonymous reviewers, who provided many useful comments during the review process.

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[6] U.S. regulations for acceptable levels of observer coverage for non-U.S. fleets have progressed from a requirement for 33% coverage of trips made by fleets with 10 or more vessels, 50% of trips on fleets of 5–9 vessels, and 100% of fleets with 1–4 vessels during 1989 and 1990 (Federal Register 12/19/89;Vol. 54 #242, p. 51918–51923), to 75% of all trips regardless of fleet size during 1991 and 1992 (10/18/90; 55 FR 42235 and 10/8/91; 56 FR 50672), to the current requirement for 100% coverage regardless of fleet size (Federal Register 1/8/92; Vol. 57, #8, p. 668).

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# Status and conservation of shearwaters of the North Pacific

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## Abstract

Of the shearwaters that breed in the North Pacific, the species in the most peril at present is Townsend's Shearwater *Puffinus auricularis*. Feral cats and pigs pose a threat on its breeding grounds. More information is needed on its current status, and that of the Black-vented Shearwater *P. opisthomelas*, most of whose nesting colonies have well-established feral cat populations. Efforts are being made to protect Newell's Shearwater *P. newelli* in the Hawaiian Islands. The single greatest threat to migrant shearwaters in the North Pacific is drift gillnet fisheries, which kill hundreds of thousands of birds annually.

## Résumé

De tous les puffins qui se reproduisent dans le Pacifique Nord, le Puffin de Townsend *Puffinus auricularis* est l'espèce la plus menacée. Les chats et les porcs retournés à l'état sauvage détruisent ses lieux de nidification. Il faut recueillir davantage d'information sur sa situation actuelle et sur celle du Puffin cul-noir *P. opisthomelas*, dont la plupart des colonies comptent également des populations bien établies de chats féraux. On s'efforce actuellement de protéger le Puffin de Newell *P. newelli* dans les îles Hawaï. La pêche au filet maillant dérivant provoque la mort de centaines de milliers d'oiseaux chaque année et constitue la plus grande menace pour les puffins migrateurs qui séjournent dans les eaux du Pacifique Nord.

## 1. Introduction

Eleven species of shearwaters (*Calonectris leucomelas* and 10 *Puffinus* species) regularly occur in the North Pacific Ocean, north of the equator. Of these, six species breed on islands north of the equator, and the other five are trans-equatorial migrants that breed in the southern hemisphere during the austral summer. Audubon's Shearwater *P. lherminieri*, a tropical species with a small fringe population breeding on the Bonin Islands, Japan (slightly north of the Tropic of Cancer), will not be considered here.

Despite their relative abundance, little is known about the biology of shearwaters in the North Pacific. Most of the published information on life histories is anecdotal and often many decades old. Remote, rugged, and inaccessible islands are the preferred breeding locales for many species. Consequently, population estimates, where available, are frequently based only on educated guesses. Within the last 20 years, however, the level of effort expended on pelagic studies of many seabirds, including shearwaters, has increased dramatically, yielding many new facts on behaviour, habitat selection, migratory routes and timing, feeding habits, and mortality.

In this paper we discuss the general biology and status of each of the shearwater species occurring in the North Pacific, consider threats and hazards both on land and at sea, and offer recommendations for future study and conservation efforts.

## 2. Species accounts

### 2.1. *Calonectris leucomelas* Streaked Shearwater

This species breeds in the far-western Pacific at many locations from the Ryukyu and Bonin islands north to Qingdao Island in the Yellow Sea, islands off northern Honshu, Japan (Melville 1984; Hasegawa 1984), and has nested on Karamizin Island in the former U.S.S.R. (Litvinenko 1976). Details on its breeding biology at Soviet and Japanese colonies are provided by Yoshida (1962, 1981), Okamoto (1972), Litvinenko (1976), and Tan (1977). The breeding season extends from February to November, and most eggs are laid in May and June. The birds nest in large, dense colonies in forested areas. After breeding, the birds disperse south to the East and South China seas, the Philippine Sea, and as far south as Borneo and New Guinea (Shuntov 1972). A few are regularly seen in winter off the north and east coasts of Australia (Blakers et al. 1984; Marchant and Higgens 1990).

Streaked Shearwaters are abundant within their range. The total population is perhaps 4–5 million individuals. Although there is no apparent cause for concern for the overall well-being of the species, "large numbers" of birds have been incidentally caught in fishing nets off Taiwan (Blackshaw 1978) and near Hong Kong (Melville 1984). Eggs and chicks have been sold in markets in Taipei (Blackshaw 1978) and Hong Kong (D.S. Melville, pers. commun.). We found no information on mortality in Japanese nearshore gillnet fisheries, but some incidental take is likely. Mass accidental deaths have taken place in anchovy crawls off Honshu, Japan (Nakamura 1974). Increased habitation of remote breeding islands by transient fishermen (Okamoto 1982) present potential threats warranting increased vigilance.

### 2.2. *Puffinus creatopus* Pink-footed Shearwater

This trans-equatorial migratory species breeds on Masatierra and Santa Clara islands in the Juan Fernandez group, Isla Mocha, and possibly a few other islands off southern Chile (Johnson 1965). What little is known about its breeding biology comes primarily from the notes of R.H. Beck (Bent 1922;

Murphy 1936) and D.S. Bullock (Murphy 1936; Johnson 1965). Birds return to the colonies in November and December, with egg-laying commencing in December and January. Fledging and departure from the islands apparently begin in March and April.

Birds disperse as far north as the Gulf of Alaska and southern Bering Sea (American Ornithologists' Union 1983). However, Vermeer et al. (1987) suggest that the west coast of British Columbia represents the northern limit of where they regularly occur. The species is essentially restricted to the eastern Pacific (Harrison 1983; Pitman 1986). Peak numbers occur in the North Pacific from July to October.

There are no population estimates, but the species is said to occur in "large numbers" on the breeding grounds (Schlatter 1984), and is certainly fairly common in migration. On the Juan Fernandez Islands the species is reportedly declining due to the destructive activities of coatimundis *Nasua narica*, feral cats, rabbits, and goats. No significant fishery-related mortality has been reported for Pink-footed Shearwaters.

### 2.3. *Puffinus carneipes* Flesh-footed Shearwater

Breeding colonies are found on islands off the south coast of western Australia, on Lord Howe Island (van Tets and Fullagar 1984), and on islands off the coast of New Zealand's North Island (Robertson and Bell 1984). In addition, 20–30 pairs breed on Saint Paul Island in the south-central Indian Ocean (Segonzac 1970).

Information on the biology of the species is provided by Warham (1958) and Serventy et al. (1971). Birds return to the colonies in late September, eggs are laid in November and December, and fledging occurs in April and May. This species is also a trans-equatorial migrant, with most of the population believed to winter in the western Pacific Ocean or Indian Ocean. The migratory route is poorly known, but some birds move along the west coast of the Americas (Murphy 1936; American Ornithologists' Union 1983; Pitman 1986). The size of the western Australia population is unknown but is estimated to be greater than 650 000 birds occupying at least 33 islands (Blakers et al. 1984). Another 20 000–40 000 pairs breed on Lord Howe Island (Fullagar and Disney 1981). The New Zealand colonies contain 50 000–100 000 pairs (Robertson and Bell 1984).

There is some concern over the destruction of lowland forests on Lord Howe Island, and the resultant reduction of breeding habitat (Robertson and Bell 1984). Introduced predators are also a problem on some islands, but some remedial efforts are under way (van Tets and Fullagar 1984). This species is a deep diver (Murphy 1936; Serventy et al. 1971) and as such is more vulnerable to fishing operations (Robertson and Bell 1984). In addition, some birds may still be taken from burrows for food. At present, none of these factors seems to present a serious or substantial threat to the species.

### 2.4. *Puffinus pacificus* Wedge-tailed Shearwater

This species is by far the most abundant and widespread breeding shearwater in the tropical Pacific and Indian oceans (Marchant and Higgens 1990; Warham 1990). Specific colony locations include Isla San Benedicto in Los Islas Revillagigedo, Mexico (at most a few thousand pairs; Pitman, unpubl. data), the Hawaiian Islands (ca. 575 000 pairs; Fefer et al. 1984; Harrison et al. 1984), Johnston Atoll (3000 birds; Amerson and Shelton 1976), Christmas Island (6000 birds; King 1974), Phoenix Islands (10 000 birds; King 1974), Taongi, Marshall Islands (12 000+ birds; King 1974), the Bonin Islands, Iwo and Marcus islands, Japan (breeds in "large numbers"; Hasegawa 1984). In Australia it breeds at numerous sites along both the west and east coasts, especially in the areas of Queensland and New South Wales (see van Tets and Fullagar 1984), with major colonies at North West Island (724 560 birds; Domm and Messersmith 1990), Heron Island (16 000 birds; Ogden 1979), Masthead Island (10 000+ birds; Jahnke 1977), Norfolk Island ("several hundred thousand birds"; Tarburton 1981), and Lord Howe Island (60 000; Fullagar et al. 1974). Other known breeding locations without estimates of numbers include Pitcairn, Gambier, Marquesas, Australs, Tonga and Niue, Fiji, and New Caledonia (see Garnett 1984). Wedge-tailed Shearwaters are also present on Jarvis and Howland islands in small numbers (Kirkpatrick and Rauzon 1986).

Breeding occurs mainly on low islands, where the species is primarily a burrow nester. Northern subtropical populations breed from April to November and southern subtropical populations breed from October to May (King 1974). Little is known about migratory movements. Rogers (1975) showed that birds departed waters off southeast Australia during the austral winter and returned in the spring to breed. Many banded birds from this population have been recovered in the Philippines, indicating that some individuals migrate to other areas. Pitman (1986) recorded large numbers of white morph Wedge-tailed Shearwaters in the far-eastern Pacific that presumably originated from central Pacific colonies. The only colony in the eastern Pacific (San Benedicto Island, see above) is small and comprises predominantly dark morphs (Jehl and Parkes 1982).

Wedge-tailed Shearwaters occupy relatively productive tropical waters, where they are often dominant in mixed-species flocks associated with foraging tunas and dolphins (Murphy and Ikehara 1955; King 1970; Au and Pitman 1986).

Although Wedge-tailed Shearwaters continue to be widespread and abundant in the tropics, it is likely that gillnet fisheries will result in some mortality. There have been some localized threats to individual breeding colonies where habitats have been altered or predators introduced (e.g., Johnston Atoll, Amerson and Shelton 1976; Jarvis Island, Rauzon 1985; Howland Island, Kirkpatrick and Rauzon 1986; Midway Island, Woodby 1988; Mariana Islands, Reichel 1991). Studies at Heron Island, Australia (Hill and Rosier 1989), suggest that well-managed development can, in some cases, be compatible with breeding colonies. However, it seems unlikely that rats can be kept off human-occupied islands indefinitely.

### 2.5. *Puffinus bulleri* Buller's (New Zealand) Shearwater

This subtropical, trans-equatorial migratory species is known to breed only on the Poor Knights Islands, off North Island, New Zealand. The total population is estimated at 2.5 million birds (Harper 1983). According to Harper (1983), birds arrive at the nesting islands in mid-September, refurbish burrows, and then leave for a 30-day pre-laying "honeymoon" at the end of October. They return to lay eggs at the end of November. The egg is incubated for approximately 51 days. Hatching occurs in mid-January and most fledglings leave the islands in early May. The majority of nests are in excavated burrows or in caverns under rocks.

By June, most of the birds have left New Zealand waters and travelled north to summer in the North Pacific (Jenkins 1988). Northward migration appears to be mainly through the western Pacific, as only small numbers have been observed migrating through the tropics in the central Pacific (Gould 1971; Cheshire 1974; Jenkins 1986). Only stragglers occur in the eastern Pacific (Pitman 1986). Migrants travel quickly through the tropics, but will temporarily join feeding flocks they encounter along the way (Gould 1971; Pitman, unpubl. data).

Significant numbers of Buller's Shearwaters arrive in the North Pacific in June. During July and August they move increasingly northwards and eastwards as far as the Gulf of Alaska (Wahl 1985). By September most of the breeding birds have once again departed for New Zealand. A large build-up off the North American west coast during September and October probably comprises mainly lingering prebreeders taking advantage of abundant food resources (Wahl 1985; Briggs et al. 1987). By November most of these have moved south also, and only occasional stragglers are reported in the North Pacific during the winter.

Buller's Shearwaters have increased dramatically since the turn of the century after introduced pigs were eliminated from one of the major nesting colonies. Harper (1983) stated that the population at Aorangi Island increased from 100 pairs in 1938 to about 200 000 pairs in 1981. This increase is apparently responsible for a widening distribution reported in recent years in New Zealand waters (Jenkins 1988) and the North Pacific (Guzman and Myres 1983; Wahl 1985). Being less inclined to dive makes this species less vulnerable to gillnet entanglement than other species of shearwaters.

### 2.6. *Puffinus griseus* Sooty Shearwater

This species breeds in large numbers on both sides of the South Pacific, with large colonies on islands around New Zealand and off southern Chile. South American colonies in the Pacific include Chiloe Island (Marin 1984), Guafo Island (min. 200 000 birds; Clark et al. 1984a), Guamblin Island (Clark et al. 1984b), and islands around Cape Horn (Murphy 1936; Johnson 1965). New Zealand hosts numerous large colonies (Robertson and Bell 1984), including the immense Snares Islands population (2 750 000 pairs; Warham and Wilson 1982). Nesting also occurs on Macquarie Island (1770 pairs; Brothers 1984). Relatively small numbers breed off Australia (Lane and White 1983), the largest colony being 1000 pairs on Tasman Island, Tasmania (Brothers 1979).

The following phenology is from Warham et al. (1982) and pertains to breeding in New Zealand, but, as pointed out by the authors, appears to apply with slight differences to all the known populations. Birds arrive at the colony in early September and eggs are laid in mid-November. After an incubation period of 53 days, chicks hatch in mid-January. Adults raise the chicks until the third week of April and then depart. Most of the chicks depart between the last week of April and the first week in May.

At the end of the breeding season birds migrate to northern oceans for the boreal summer. The majority of birds that migrate to the North Pacific seem to make a clockwise circumnavigation, moving north past Japan in the spring, crossing south of the Aleutian Islands in summer, and then proceeding south along the west coast of the Americas during the fall (Murphy 1936). However, much still remains to be learned about this species' movement patterns (Briggs and Chu 1986). For example, flocks containing as many as 90 000 birds have been observed along the west coast of British Columbia in early May (Vermeer and Rankin 1984a).

There seems to be no immediate serious threat to birds at breeding colonies in New Zealand. Efforts are being made to eliminate introduced predators from many of the important seabird islands (Robertson and Bell 1984; Veitch 1985). Considerably less is known, however, about the status, or even distribution, of colonies off southern Chile.

The major hazard for birds at sea in the North Pacific at this writing is probably incidental take by gillnet fishing. Relatively few Sooty Shearwaters were killed by drift gill nets in the high-seas Japanese salmon mothership fishery during 1981–1984, presumably because the fishery operated north of the main migratory route for this species (Jones and DeGange 1988). DeGange et al. (1985) estimated that Sooty Shearwaters constituted only 0.3% of the total incidental bird kill in that fishery between 1981 and 1984. However, the preliminary information on the North Pacific drift gillnet fishery for squid, which operates at a lower latitude, suggests Sooty Shearwaters may currently sustain losses of up to 400 000 individuals annually (Gjernes et al. 1990). There is also very little specific information available on incidental shearwater mortality in gillnet fisheries off California (Herrick and Hanan 1988), where the species numbers in the millions at times and is often the most abundant seabird species present during the summer months (Briggs et al. 1987). A cooperative observer program operated by the National Marine Fisheries Service and California Department of Fish and Game began in spring 1990, and observers placed on gillnet boats have been collecting data on seabird mortality during fishing operations.

### 2.7. *Puffinus tenuirostris* Short-tailed Shearwater

The Short-tailed Shearwater breeds only in Tasmania and on islands off southeast Australia. Skira et al. (1985, and references therein) estimated 11.4 million burrows from 167 colonies in Tasmania, 1.45 million burrows in Victoria, 1.5 ± 0.5 million burrows in South Australia, 25 700 breeding pairs in New South Wales, and 250 burrows in Western Australia. The total world population is roughly 23 million birds.

According to Serventy (1967), birds first arrive on the breeding islands the last week in September and for the next four weeks they prepare their burrows. After a two-week pre-laying exodus, most egg-laying occurs in the last week of November. Males and females share incubation duties in shifts of 10–16 days. The single egg hatches in about 53 days and the chicks depart from mid-April to the first week in May, after spending about 94 days in the burrow (Skira et al. 1985).

The trans-equatorial migration of this species apparently takes it north through the far-western Pacific past Japan to its main wintering (austral) grounds off the Aleutian Islands and in the Bering Sea. The return migration, in August and September, is thought to take place primarily through the central Pacific (Lindsey 1986; Pitman 1986; Warham 1990).

Populations at managed breeding colonies appear stable despite the annual combined commercial and noncommercial harvest of an estimated 700 000 chicks (Skira et al. 1985; Skira 1987). Substantial numbers of Short-tailed Shearwaters perish each year in high-seas drift gillnet fisheries in the North Pacific Ocean (King 1984; DeGange et al. 1985; Atkins and Heneman 1987; Jones and DeGange 1988; Gjernes et al. 1990). The incidental kill is in the hundreds of thousands of birds annually, and undoubtedly millions have perished since the fisheries began. Although the species is apparently still abundant, the combined effects of incidental kill, harvesting, and natural mortality could eventually decimate and jeopardize the species.

### 2.8. *Puffinus nativitatis* Christmas (Island) Shearwater

Confined to the Pacific Ocean, this little-known species breeds at Easter Island (Johnson et al. 1970), Oeno, Ducie, and likely Henderson islands, the Pitcairn group (Williams 1960; Schubel and Steadman 1989), Gambier (Thibault 1973), the Tuamotus and Austral group (Holyoak 1973), Taongi Atoll in the Marshall Islands (Amerson 1969), the Marquesas (King 1967), Johnston Atoll, and the Hawaiian Islands (Harrison et al. 1984); it apparently formerly bred on Wake, Marcus, and the Bonin islands (King 1967).

Information on population sizes is scant. Ashmole and Ashmole (1967) reported the Christmas Island population to be 7000 birds, making it the largest known colony. Harrison and Jehl (1988) estimated 2500 pairs nesting at Sala y Gomez, Chile. Fefer et al. (1984) reported a total of 2960 pairs nesting in the northwest Hawaiian Islands, and Amerson and Shelton (1976) estimated 30 individuals on Johnston Atoll. The Easter Island population consisted of 80–100 pairs in 1968 (Johnson et al. 1970). Comprehensive accurate data are lacking, but a world population on the order of a few tens of thousands seems likely.

Breeding is year-round on equatorial Christmas Island (Schreiber and Ashmole 1970), but seasonal in the more subtropical Hawaiian Islands, where adults return to colonies in March and fledge most of their young by late September (Richardson 1957; Fefer et al. 1984). Nesting usually occurs in fairly open areas, in rock crevices or under vegetation (Shallenberger 1984). Unlike most other species of *Puffinus*, Christmas Shearwaters do not nest in burrows.

Open ocean waters are preferred by this species, and it is uncommon but regular throughout the eastern and central tropical Pacific (King 1967; Pitman 1986). Although there is no published information to suggest that populations undergo any regular migrations within the tropics, moderate numbers are usually present off the coasts of central and southern Mexico and Central America (Pitman, unpubl. data), more than 4500 km from the nearest known nesting colony, suggesting regular movements to that area.

There appear to be no major threats to this species at sea. Breeding colonies in Hawaii were adversely affected by introduced rabbits, but seemed to recover when the rabbits were eliminated (Harrison et al. 1984). The Johnston Atoll population declined from 400 to 30 birds after the island was occupied by the military and a paved airstrip was installed (Amerson and Shelton 1976). There is concern for the small Midway Island population (25–50 pairs; Fefer et al. 1984), which is currently threatened by introduced black rats *Rattus rattus* (Woodby 1988).

### 2.9. *Puffinus opisthomelas* Black-vented Shearwater

The only documented breeding locales of this species are at Isla Guadalupe, Isla Natividad, and Islas San Benito, all off the west coast of Baja California, Mexico (Everett 1988a). On Isla Natividad, the shearwaters burrow in the sandy soil covering most of the southeast portion of the island. The only known active colonies at Isla Guadalupe are on two offshore islets, Isolote Negro and Isolote Afuera. Anthony (1900) reported breeding on the main island of Guadalupe, but exact locations have never been determined. The introduction of cats to the island may have resulted in abandonment of these breeding grounds. At Islas San Benito, nests have been found on all three islands, but nowhere in any large concentration. At both Guadalupe and the San Benitos, birds occupy natural holes in the lava or crevices, or they burrow under large boulders.

Based on the limited available information, breeding colonies are occupied by mid-January and the peak of laying is in early April. By June many burrows have a chick, and fledging occurs from late June through August (Everett 1988a).

Black-vented Shearwaters primarily inhabit coastal waters, up to 25 km offshore. During the breeding season they are uncommon in areas other than the Pacific coast of Baja California. When breeding is concluded many disperse to the north and south. Typically, birds that head north move into the Southern California Bight, from Point Conception to Islas Los Coronados. During some years they are found as far north as Monterey Bay. Stragglers have been recorded as far north as British Columbia (Campbell et al. 1990). South of Cabo San Lucas there are few data, and the situation is complicated because of the occurrence of mixed flocks of *P. opisthomelas/auricularis* (Jehl 1974, 1982).

The estimate of population size is speculative, based primarily on observations and counts of birds staging at dusk near the breeding islands. The number of pairs is likely in the following range: Isla Guadalupe 500–2500, Islas San Benito 250–500, Isla Natividad 2500–5000. Feral cats are established on most of the breeding islands, and all visitors to these colonies have reported widespread destruction. Huge flocks such as those reported at the turn of the century (Anthony 1896; Grinnell 1897) are no longer seen. Gillnet fisheries have expanded off the west coast of Baja California in recent years, but the impact of these operations (Atkins and Heneman 1987) on the Black-vented Shearwater population is completely unknown.

### 2.10. *Puffinus auricularis* Townsend's Shearwater

Isla Socorro and Isla Clarion in Las Islas Revillagigedo, off the west coast of Mexico, are the only known recent nesting locales for this species, which also formerly bred on Isla San Benedicto in the same group (Jehl 1982; Everett and Anderson 1991). Jehl (1982) most recently summarized the scant available information on the biology of this endangered species. The birds apparently return to the islands beginning in mid-November. Laying probably begins in January, as large young have been found in late April.

The pelagic range of this species is among the smallest of any seabird, extending in a narrow band of subtropical water between 11 and 23°N, from the Mexican mainland to about 400 nautical miles southwest of Isla Clarion (Pitman 1986).

There has been no census on either breeding island, but Jehl estimated 1000 pairs on Isla Socorro in 1981. The population on Isla Clarion in 1986 was thought to be at best slightly less (Everett, unpubl. data). A massive volcanic eruption in 1952 eliminated the colony on Isla San Benedicto, and the other breeding islands are suffering the effects of introduced predators and herbivores. Pigs and rabbits were introduced to Clarion in 1979 (Everett 1988b), and feral cats have long been observed on Socorro (which is much larger than Clarion) from sea level to the summit of this rugged volcanic island. All visitors (including Pitman in 1988) report mass destruction of shearwaters, feathers in scat, and similar signs of decline. A visit to Clarion in May 1990 (Santaella and Sada, in press) raised the disturbing possibility that the species has now been extirpated from the island.

There is a modest program under way to rid Socorro of cats, but this will be a difficult and perhaps impossible task given the large size of the island and the mostly hostile terrain (see Veitch 1985). Preserving the species on Clarion may be more feasible, if remedial steps are undertaken soon (see recommendations below). Based on observations in May 1990 of birds flying inland at dusk (Santaella and Sada, in press), it is possible the species may be recolonizing Isla San Benedicto.

2.11. *Puffinus newelli* Newell's Shearwater

Once common on several of the Hawaiian Islands, Newell's Shearwater is now known to breed only on the island of Kauai. Recent observations suggest that small colonies may still exist on other main Hawaiian Islands (Harrison 1990). Although the species was thought to be extinct for many years, a documented record was obtained in 1954 (Richardson 1955), and by 1967 the nesting grounds were rediscovered (Sincock and Swedberg 1969). King and Gould (1967) summarized historic information on the biology of the species. The breeding season extends from April to November (Harrison 1990), after which at least some of the population disperses to the north and southeast (Pitman 1986).

The most recent population estimate suggests that up to 6000 pairs inhabit Kauai (Harrison et al. 1984). The species' decline has been blamed on predation by pigs, cats, mongooses, rats, and Barn Owls *Tyto alba*. Fire has also destroyed some colonies. Another significant problem has been coastal street lights, which attract and disorient fledglings on their first flights to the ocean. The problem, most serious on moonless nights, has been somewhat mitigated by shielding upward radiation of light and by an intense salvage program to find and return stranded birds to the sea. Over 20 000 birds have been assisted in this manner (Reed et al. 1985; Tefler et al. 1987; Reed 1987; Harrison 1990).

In addition, cross-fostering with Wedge-tailed Shearwaters has been attempted in order to encourage establishment of new colonies on offshore islets free from terrestrial predation and light distraction (Byrd et al. 1984). Results of this experiment, in terms of birds returning to the foster colonies to breed, are as yet unavailable.

## 3. Hazards for shearwaters at sea

At present, the most serious threat to shearwaters at sea is undoubtedly incidental mortality in drift gillnet fisheries (King 1984; DeGange et al. 1985; Atkins and Heneman 1987). The species suffering the greatest losses is apparently the Short-tailed Shearwater, whose high-latitude migration places it in regions heavily fished (Jones and DeGange 1988). Its pursuit-diving habits also enhance its susceptibility to entanglement. Other diving species (e.g., Wedge-tailed and Christmas shearwaters) are not as gregarious or occur in areas of lower fishing effort. Although the Japanese high-seas salmon driftnet fishery has recently reduced its kill, concern is escalating regarding the incidental take in the North Pacific squid *Ommastrephes bartrami* fishery (King 1984). Preliminary results from a pilot observer program in this fishery are alarming, suggesting mortality in the hundreds of thousands for Sooty and Short-tailed shearwaters (Gjernes et al. 1990). At this writing, an expanded observer program is under way, and a call for a ban on all drift gillnet fishing has been made by the United Nations. The Japanese have agreed to cease their driftnet fisheries, but other nations such as Korea and Taiwan have yet to comply. Although the numbers of shearwaters killed in fishery operations have been massive, there is no current evidence of population declines for the species involved. However, shearwaters are notoriously difficult to census, so the situation heightens the need for monitoring breeding colonies.

Although competition with commercial fisheries may present problems for other groups of seabirds (Furness and Ainley 1984; Furness and Monaghan 1987), we know of no serious prey depletions adversely affecting shearwaters.

Oil spills also clearly present a threat to shearwaters, especially those inhabiting regions where shipping or extraction activities are high. After the *Exxon Valdez* spill in Alaskan waters in March 1989, many thousands of dead shearwaters were recovered, although the number of mortalities directly related to the spill is not clearly known (Piatt et al. 1990).

Ingestion of plastics at sea is a concern for many species of seabirds (Furness and Monaghan 1987), with both northern and southern hemisphere procellariiforms being heavily contaminated. The primary difficulty with plastics ingestion seems to be a reduction of gizzard and stomach capacity, with possible resultant malnutrition or starvation (Conners and Smith 1982; Ryan 1988). This has not, however, been demonstrated in shearwaters, which apparently have the ability to regurgitate undigestible items (e.g., squid beaks). At this time, plastic ingestion does not appear to be a significant problem for shearwaters.

## 4. Hazards for shearwaters on land

Many seabirds, including shearwaters, encounter problems resulting from habitat destruction and disturbance when they return to land to breed (Vermeer and Rankin 1984b). This can result directly from human activities or be a consequence of the introduction of alien animals. For species under consideration here, direct human disturbance has apparently been a factor in the declines of several tropical colonies. Occupation of remote islands by the military, especially where airstrips have been installed, has proven destructive to shearwaters (King 1973; Amerson and Shelton 1976; Rauzon 1985). Light attraction, discussed above, is a serious problem for Newell's Shearwater. Remedial action seems to be helping, and, fortunately, this problem is unlikely to affect most other shearwater species. The introduction of pigs and rabbits to Isla Clarion (Everett 1988b) has dramatically altered the island's landscape. The soil destabilization and erosion caused by their activities may destroy the breeding grounds of Townsend's Shearwater.

The most serious problem facing shearwaters on land is predation by introduced animals. The general impacts are well documented (Moors and Atkinson 1984), and need not be reiterated here. Species at the highest risk are those with small populations and few colonies. In addition, shearwaters breeding on high, thickly vegetated islands stand a more substantial likelihood of depredation because predators are more likely to become established in lush areas with alternative food sources available when shearwaters are absent. Many of the species discussed here suffer from predation, but Townsend's Shearwater, Newell's Shearwater, and possibly Black-vented Shearwater seem to be experiencing serious population declines as a result.

## 5. Recommendations

(1) Immediate action is required to rid Isla Clarion of pigs, then rabbits, in order to secure the island as a breeding locale for Townsend's Shearwater. Efforts are under way to remove feral cats from Isla Socorro, but that island is large and the terrain extremely difficult. Considering these problems it appears unlikely that the cat eradication program there will be successful in the near future.

(2) All drift gillnet fisheries should be banned or closely monitored and regulated. In cases where large numbers of shearwaters are being killed, fishing moratoriums should be implemented until it can be determined that serious seabird population declines are not resulting. This cannot be accomplished without careful censuses at breeding colonies over a period of several years at minimum.

(3) The population status and vulnerability of Black-vented Shearwater colonies should be determined, with implementation of appropriate remedial actions and policies if necessary.

(4) The multi-faceted program to protect and preserve Newell's Shearwater in Hawaii should be continued, including increased efforts to locate additional colonies.

(5) Predator removal programs currently in progress in New Zealand, Australia, and the central Pacific should be continued as long as required to achieve eradication.

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# Preliminary Winter Abundance Estimates for Cetaceans Along the California Coast Based on a 1991 Aerial Survey

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## ABSTRACT

We present the results of an aerial line transect census of cetaceans along the California coast during March and April 1991. This survey was the first of two aerial surveys designed to estimate cetacean abundance within approximately 100–150 n.miles (185–278km) of the coast. A primary team of two observers searched through bubble windows which allowed an unobstructed view of the trackline directly underneath the aircraft. A third, semi-independent observer searched through a belly window and made observations of animals that were missed by the primary team. A total of 155 sightings were made of a minimum of 14 cetacean species (some animals could only be identified to higher taxa). Of those groups that were on the trackline, the fraction seen by at least one team, $g(0)$, was estimated to be at least 0.821 for groups of $\leq$10 small cetaceans, 0.956 for groups of >10 small cetaceans and 0.977 for medium and large cetaceans. Estimates of abundance using these correction factors are 277,783 common dolphins (CV=0.46), 10,506 Risso's dolphins (CV=0.48), 46,334 Pacific white-sided dolphins (CV=0.78), 13,362 northern right whale dolphins (CV=0.41), 1,236 harbor porpoise (CV=0.45), 5,832 Dall's porpoise (CV=0.28), 4,011 bottlenose dolphins (CV=0.62), 117 minke whales (CV=0.68), 1,720 gray whales (CV=0.42), 405 humpback whales (CV=0.42), 87 killer whales (CV=0.76), 56 sperm whales (CV=1.07), 505 beaked whales (CV=0.44) and 59 fin/sei/Bryde's whales (CV=1.00).

KEYWORDS: SURVEY-AERIAL; NORTH ATLANTIC; ASSESSMENT; COMMON DOLPHIN; RISSO'S DOLPHIN; WHITE-SIDED DOLPHIN; RIGHT WHALE DOLPHIN; HARBOUR PORPOISE; DALL'S PORPOISE; BOTTLENOSE DOLPHIN; MINKE WHALE; GRAY WHALE; HUMPBACK WHALE; KILLER WHALE; SPERM WHALE; BEAKED WHALE; FIN WHALE; SEI WHALE; BRYDE'S WHALE.

## INTRODUCTION

Under the 1988 Amendment to the US Marine Mammal Protection Act, incidental mortality of marine mammals in commercial fishing operations was authorised for the five-year period 1988–93. During this period, additional data had to be collected on the affected marine mammal species in order to provide a basis for future management decisions. Recent estimates of incidental marine mammal mortality in US west coast gillnet fisheries have been obtained through the National Marine Fisheries Service (NMFS) observer program, which began in 1990 (Perkins *et al.*, 1992; Lennert *et al.*, 1993); however, recent estimates of cetacean abundance in the fishery area are lacking. For many of the common species of cetaceans in California, the only available population estimates are over 10 years old (Dohl *et al.*, 1978; 1983) and statistical confidence limits are available only for common dolphins, *Delphinus delphis* (Dohl *et al.*, 1986). For future management considerations, new abundance estimates, including statistical confidence limits, are necessary.

In 1991 and 1992, NMFS conducted a series of two aerial surveys (March-April 1991 and February-April 1992) and one ship survey (August-November 1991) along the California coast. Standard line transect methods were used from both platforms, and the surveys were designed to yield a target level of precision (coefficient of variation (CV) < 36%) in the abundance estimates of the most common species. Due to the pronounced seasonality in the California Current, and evidence of seasonality in the abundance of common dolphins (Dohl *et al.*, 1986), separate abundance estimates were deemed appropriate for winter (cold water) and summer (warm water) conditions. The survey periods were chosen based on climatic atlases of the California coast which show that, on average, March/April have the coldest sea surface temperatures, and September/October the warmest.

This paper presents the results of the 1991 aerial survey. Although the results are preliminary (the survey design indicated that two aerial surveys would be required to obtain an acceptable level of precision) we believe it is important to present them at this time given the lack of recent estimates for the majority of cetacean species in California. Final results will be presented for the two combined aerial surveys and for the ship survey when all data have been compiled and analysed.

## SURVEY METHODS

### Study area

The study area (Fig. 1) extends beyond the continental shelf edge along the California coast, to roughly the 3,000–4,000m depth isobath. This study area was defined on the basis of fisheries that are known to take marine mammals; the boundaries do not reflect the distributional boundaries of any known marine mammal populations. It encompasses all of the known coastal gillnet fishing area, based on effort data from the California Department of Fish and Game (CDFG). In central and northern California, this extends from the coast to approximately 100 n.miles (185km) perpendicular distance offshore. In the Southern California Bight, the study area is bounded by the US/Mexico border in the South and extends out to approximately 150 n.miles (278km) offshore. It then follows a straight line northwestward to a point 100 n.miles (185km) off Point Conception, connecting with the outer boundary of the central California area (see Fig. 1).

### Transects

A total of 154 transects form two approximately uniform, overlapping grids with lines spaced roughly 45–50 n.miles (83–93km) apart. This yields an overall grid with lines spaced approximately 22–25 n.miles (41-46km) apart (Fig. 1). The location of the grid was chosen without reference to

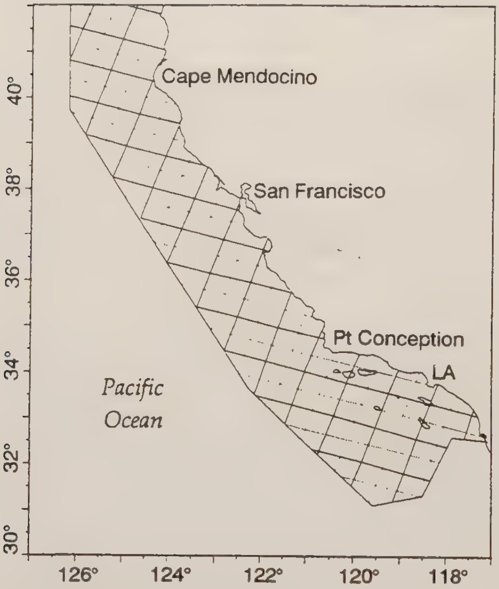

Fig. 1. Study area with two overlapping transects grids. The solid line represents Grid 1, the dotted line Grid 2.

specific areas or topographical features. They are oriented to reduce sun glare during the surveys while providing approximately uniform coverage of the study area and minimising non-survey travel time. Survey direction along transects was chosen to minimise glare, generally in a northeast or northwest direction. To avoid potential differences in regional coverage, an attempt was made to complete all transects of the first grid, providing coarse coverage of the entire study area, before beginning the second grid.

### Equipment and procedures

The survey platform was a twin-engine turbo-prop *DeHavilland* Twin Otter, with capacity for five scientists and two pilots. Surveys were conducted at approximately 700ft (213m) altitude and 100 knots (167–185km/hr) airspeed. The surveys were designed to obtain abundance estimates for cetaceans, but pinnipeds were recorded when seen farther than 10km from land to provide information on their offshore distribution. Turtle sightings were also recorded. Two 'primary' observers searched through bubble windows on the left and right sides of the aircraft. These windows allowed viewing to the side and directly beneath the aircraft with at least 10° of overlap between sides. To achieve higher sighting efficiency near the trackline, observers searched for cetaceans only out to 1,000m perpendicular distance (12° declination angle).

A round 18in (46cm) viewing hole in the belly of the aircraft was used for monitoring of the trackline by a 'secondary' observer. This viewing port provided visibility of the trackline between 55° left and 55° right declination, overlapping considerably with the primary observers. The secondary observer reported cetaceans missed by the primary team, so that the fraction of animals missed on the trackline could later be estimated. A fourth person recorded all sighting, effort and environmental data. Approximately every 30 minutes, the five scientists rotated between these four active positions and one resting position. All observers had previous experience in identifying cetacean species from aerial and/or shipboard surveys.

### Data recording

A laptop computer connected to a *LORAN* navigational receiver was used to record survey data. During the survey, a continuous record of position (updated every few seconds), altitude, airspeed and survey conditions was maintained. Conversation in the aircraft was recorded on a central cassette recorder to provide a complete record of activities. In addition, observers recorded individual sighting information into personal notebooks.

### Environmental conditions

Environmental conditions were recorded throughout the survey whenever changes occurred. Sea state was recorded using the Beaufort scale; surveys were conducted only in sea states 0–4. Sky condition was recorded as a percentage of cloud cover between the viewing area and the sun. Glare (due to sun or cloud reflections) was recorded separately by each observer as a percentage of the viewing area obscured. Water colour was categorised as dark blue, light blue, or green, based on comparison with colour plates of known hue and intensity. Presence/absence data was recorded for haze below the aircraft and for kelp on the water surface.

### Sighting procedures

When sightings were made, the aircraft's position was recorded along with information on species identification, the observer who made the sighting and the declination angle to the center of the school (measured with a clinometer). All observers then concentrated on identifying the sighted species and estimating school size while the aircraft circled over the animals. School size was defined to include the animal(s) initially sighted as well as any additional subgroups judged to belong to the same school (i.e. travelling in the same direction or belonging to the same feeding aggregation). Fluorescein dye markers were dropped as necessary to aid in the relocation of animals. Navigation and position features in the data entry program were also used to relocate animals, and to return to the same location on the trackline after all sighting information had been collected. Any additional schools sighted while diverted from the transect were recorded as 'off effort' sightings and were not used for abundance estimation.

Species identification was discussed and agreed upon by all observers. When it was not possible to identify animals with certainty, a code or combination of codes reflecting the possible identification of the animals was entered. A flowchart of the species codes used is shown in Fig. 2. High, low and best estimates of school size were recorded separately by all observers who were able to obtain an estimate. To avoid influencing each other, the observers wrote their estimates into personal notebooks without discussing them. At the end of the day, the survey leader entered all estimates into the data files.

Sighting procedures were essentially the same for the primary and secondary observers, except that the secondary observer waited approximately 10 seconds after sighting animals before announcing them, in order to ensure that they had passed the field of view and were missed by the primary team. Additionally, due to space

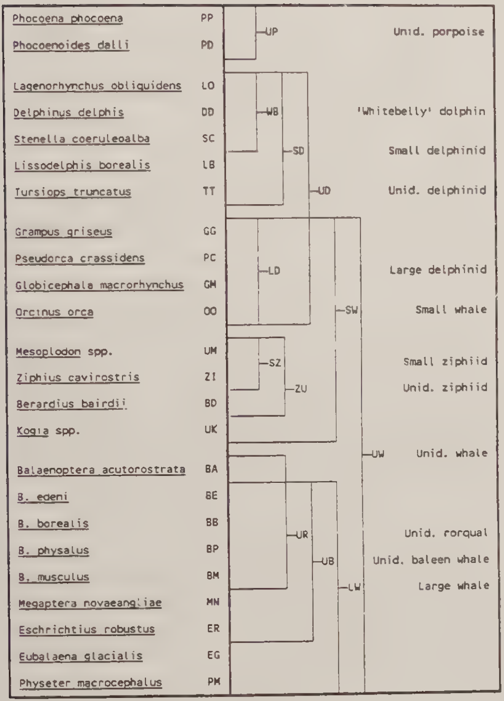
Phocoena phocoena PP
Phocoenoides dalli PD
Lagenorhynchus obliquidens LO
Delphinus delphis DD
Stenella coeruleoalba SC
Lissodelphis borealis LB
Tursiops truncatus TT
Grampus griseus GG
Pseudorca crassidens PC
Globicephala macrorhynchus GM
Orcinus orca OO
Mesoplodon spp. UM
Ziphius cavirostris ZI
Berardius bairdii BD
Kogia spp. UK
Balaenoptera acutorostrata BA
B. edeni BE
B. borealis BB
B. physalus BP
B. musculus BM
Megaptera novaeangliae MN
Eschrichtius robustus ER
Eubalaena glacialis EG
Physeter macrocephalus PM
UP
WB
SD
UD
LD
SW
SZ
ZU
UW
UR
UB
LW
Unid. porpoise
'Whitebelly' dolphin
Small delphinid
Unid. delphinid
Large delphinid
Small whale
Small ziphiid
Unid. ziphiid
Unid. whale
Unid. rorqual
Unid. baleen whale
Large whale

Fig. 2. Flowchart of species identification codes used during the 1991 aerial survey. Not all species were seen.

limitations in the belly viewing port, the secondary observer estimated sighting angles from marks previously applied to the window, rather than using a clinometer.

## ANALYTICAL METHODS

### Data stratification

The study area was divided into four *a posteriori* geographic areas based on survey coverage and species distributions. This was necessary because we were not able to complete both grids in all areas and the resulting coverage was not uniform throughout the study area. As species distributions were also not uniform, it was inappropriate to estimate abundances over the entire region.

Although environmental conditions such as sea state and percentage of cloud cover were recorded throughout the survey and have been shown to influence cetacean sighting rates (Holt and Cologne, 1987; Forney *et al.*, 1991), it was not possible to stratify the data by these criteria due to insufficient sample sizes. It is expected that addition of data from the second survey year will provide sufficient information to evaluate the effects of environmental conditions.

Sightings of unidentified species have either been excluded from abundance calculations (Wade and Gerrodette, 1992), or they have been assigned to individual species based on the proportion of sightings of each species (Holt and Sexton, 1989; Wade and Gerrodette, 1993). Neither approach is satisfactory for this analysis due to the small number of sightings made during the survey and the non-uniform distribution of some species throughout the study area. To maximise sample sizes without relying on imprecise estimates of species proportions, sightings of unidentified species were assigned a species code based on the geographically closest identified sighting of a candidate species (see Fig. 2). For example, a school of dolphins identified as 'whitebellies' (indicating they were either Pacific white-sided (*Lagenorhynchus obliquidens*), striped (*Stenella coeruleoalba*) or common dolphins), was assigned to one of these three based on the identity of the species which had the closest identified sighting. Due to the rarity of beaked whale sightings, and the general difficulty in resighting and identifying them to the species level during surveys, only a combined abundance estimate was obtained for this group.

The small number of sightings also made it necessary to pool distributions of perpendicular sighting distances to estimate the detection probability density function for line transect calculations. Other researchers have pooled across species or species stocks with similar sighting characteristics (Holt and Sexton, 1989; Wade and Gerrodette, 1992). Sighting characteristics are generally evaluated based on body size, group size, behaviour, associated animals and other sighting cues. In particular, group size is known to influence detectability of groups (Drummer, 1985; Holt and Sexton, 1989), so only species with similar group sizes should be pooled.

Preliminary groups were created based on considerations of school size, body size and behaviour. These groups were then evaluated using a Kolmogorov-Smirnov test, and only if distributions of perpendicular distance were not significantly different from one another were the groups pooled. This resulted in the following three species/group size categories for abundance estimation: (1) small cetacean groups with 1–10 animals; (2) small cetacean groups with more than 10 animals; and (3) medium and large cetaceans. The species in these groups are given in Table 1.

Table 1

Assignment of species to three species/group size categories for estimation of f(0) and g(0). N = number of sightings in each category.

| Species | Group size | N | f(0) | g(0) |
|---|---|---|---|---|
| **Small cetaceans** | | | | |
| *Delphinus delphis*<br>*Grampus griseus*<br>*Lagenorhynchus obliquidens*<br>*Lissodelphis borealis*<br>*Phocoena phocoena*<br>*Phocoenoides dalli*<br>*Tursiops truncatus* | 1-10<br>>10 | 63<br>26 | 4.15<br>2.37 | 0.821<br>0.956 |
| **Large cetaceans** | | | | |
| *Balaenoptera acutorostrata*<br>*Eschrichtius robustus*<br>*Megaptera novaeangliae*<br>*Orcinus orca*<br>*Physeter macrocephalus*<br>*Balaenoptera* sp.<br>Ziphiid whales | 1-10 | 37 | 2.32 | 0.977 |

In summary, the data for each species were divided into either four or eight strata, defined by four areas and one or two group size categories. Species-specific abundances were calculated separately for each stratum and then combined to obtain overall population estimates.

**Abundance estimation**

Line transect methods (Burnham *et al.*, 1980) were applied to estimate abundances separately for each stratum. A modification of the standard formula used to estimate the density of animals, corrected for the probability of missing animals on the trackline (Buckland *et al.*, 1993), was used here to estimate the abundance of each species:

$$N = \sum_{j=1}^{3} \sum_{i=1}^{4} \frac{n_{i,j} s_{i,j} f_j(0)}{2 L_i g_j(0)} A_i, \qquad (1)$$

where

$N$ = estimate of the total number of animals of the species in the study area;

$n_{i,j}$ = number of sightings of the species in Area $i$ and species/group size category $j$;

$s_{i,j}$ = average group size of the species in Area $i$ and species/group size category $j$, calculated as the total number of animals in all groups divided by the number of groups sighted;

$f_j(0)$ = the probability density function evaluated at zero perpendicular distance for species/group size category $j$;

$g_j(0)$ = the probability of detecting a group of animals on the trackline for species/group size category $j$;

$L_i$ = the length of transect surveyed in Area $i$ (in km);

$A_i$ = the size of Area $i$ (in km$^2$).

Values for $f(0)$ were obtained for each species/group size category by fitting the distribution of all perpendicular sighting distances (primary and secondary) to the Hazard rate model with the program *HAZARD* (Buckland, 1985).

**Correction for missed animals,** $g(0)$

Standard line transect theory generally sets $g(0) = 1$, assuming that all animals on the trackline are seen. However, in aerial surveys for cetaceans, animals on the trackline are likely to be missed due to two factors: (1) animals at the surface may not be seen by the observers; and (2) animals which are submerged when the aircraft passes cannot be seen by observers. These two types of visibility bias have been called perception bias and availability bias, respectively (Marsh and Sinclair, 1989).

Availability bias has been corrected in the analysis of harbor porpoise line transect data, based on studies of dive patterns of individual animals (Barlow *et al.*, 1988; Calambokidis *et al.*, 1992). However, the proportion of time a school is visible will depend not only on dive patterns of individuals, but also on the size of the group (Holt and Cologne, 1987). Separate correction factors for different species and/or school sizes are difficult and expensive to obtain, and are not currently available. In this analysis, no correction for availability bias could be made.

Perception bias in line transect surveys has been addressed through independent observer experiments, which use additional observers on secondary platforms, such as additional aircraft, vessels or land-based observation points (Hiby and Hammond, 1989; Calambokidis, 1990), or add a second observer team on a single survey platform (Butterworth and Borchers, 1988; Hiby and Hammond, 1989; Øien, 1990).

In this study, the first approach was not feasible due to the high cost and logistic problems involved in having a second aircraft or vessel nearby to identify missed animals. Furthermore, the need to circle over each group of animals sighted for identification and enumeration made it impossible to have two fully independent observer teams within the aircraft. For these reasons, we opted for a partially independent observer design, wherein the secondary observer called out sightings only after they had been missed by the primary team. This enables estimation of a maximum correction factor for the fraction of animals missed by both teams.

The fraction of animals seen on the trackline by both teams combined, $g_{Tot}(0)$, can be expressed as:

$$g_{Tot}(0) = g_P(0) + g_S(0)\,(1\text{-}g_P(0)) \qquad (2)$$

where the subscripts $P$ and $S$ represent the primary and secondary teams, respectively. Although both $g_{Tot}(0)$ and $g_S(0)$ are unknown, the ratio $g_{Tot}(0)/g_P(0)$ can be estimated as:

$$\frac{g_{Tot}(0)}{g_P(0)} = \frac{n_{Tot}\, f_{Tot}(0)}{n_P f_P(0)} \qquad (3)$$

where

$n_{Tot}$ = number of sightings made by the primary and secondary teams combined;

$n_P$ = number of sightings made by the primary team;

$f_{Tot}(0)$ = probability density function evaluated at zero perpendicular distance for primary and secondary sightings combined;

$f_P(0)$ = probability density function evaluated at zero perpendicular distance for primary sightings.

We assume that the secondary observer misses no more than the primary observers on the trackline ($g_S(0) \geq g_P(0)$). Therefore, the following inequality, in terms of the known ratio $g_{Tot}(0)/g_P(0)$, can be derived from Equation (2) for the expected fraction of animals on the trackline seen by at least one observer team:

$$g_{Tot}(0) \geq \left(2 - \frac{g_{Tot}(0)}{g_P(0)}\right) \frac{g_{Tot}(0)}{g_P(0)} \qquad (4)$$

The two sides are equal when $g_S(0) = g_P(0)$. Using the above equations, the overall probability of detecting a group of animals on the trackline, $g_{Tot}(0)$, was estimated for each of the three species/group size categories. Because the view of the trackline from the belly (secondary) observer position is better than from the side (primary) positions, $g_{Tot}(0)$ is expected to represent the minimum proportion seen.

**Variance estimation**

Variance in the abundance estimates was calculated using bootstrap techniques applied to the complete data set. The data were subdivided by area into segments of effort of equal length. To investigate possible effects of the choice of segment length on estimates of variance, values of 5km, 10km, 15km and 20km were tested. The segments were drawn randomly with replacement until the total number of kilometers actually surveyed in each area was reached. This process was repeated 1,000 times for each segment length.

Each replicate was treated and analysed as a separate survey. Sightings were first stratified into the three above species/group size categories. Individual values for $n$ and $s$ were calculated, and $f(0)$ was estimated with the program *HAZARD*. The correction factor $g(0)$ estimated for the actual survey data was used for all bootstrap calculations, and was assumed to be known without error. Uncorrected (assuming $g(0)$=1) and corrected (using the estimated correction factor $g(0)$) abundance estimates for each species were then calculated for each replicate. The variance, coefficient of variation and percentile confidence limits (Buckland, 1984) were obtained from the distribution of the 1,000 bootstrap abundance estimates using standard formulae.

## RESULTS

A summary of all completed survey effort, stratified by Beaufort sea state and percentage cloud cover, is shown in Table 2. Due to unusually stormy weather during the survey period, only approximately 85% (5,309km) of transect Grid 1 and 27% (1,724km) of Grid 2 were completed, for a total of 7,033km. Fig. 3 shows the completed transects and the four *a posteriori* areas used for stratification. Approximately uniform effort was achieved within each area stratum. A total of 126 cetacean sightings were made while on effort (actively searching), and an additional 29 sightings were made while off effort (in transit or circling). The locations of all 155 cetacean sightings made during the survey are plotted in Fig. 4. Sighting information stratified by area and species is summarised in Table 3.

Positive species identification was not possible for 21 of the 126 'on effort' sightings. Four of these sightings were identified as ziphiid whales, for which a combined abundance estimate will be obtained, and no individual species assignment is required. For the remaining 17 sightings, assignments to individual species are shown in Table 4. In one case, the animals were identified as belonging to the genus *Balaenoptera* and could be narrowed down to one of three species: fin whale (*B. physalus*), sei whale (*B. edeni*) or Bryde's whale (*B. borealis*). However, none of these three species were otherwise sighted during the survey, and no individual species could be assigned.

Table 2

Survey effort (in kilometers) stratified by sea state and % cloud cover.

| | Beaufort sea state | | | | |
|---|---|---|---|---|---|
| % Cloud cover | 0&1 | 2 | 3 | 4 | Total |
| 0-24 | 211 | 911 | 1,917 | 1,339 | 4,378 |
| 25-49 | 26 | 66 | 96 | 85 | 273 |
| 50-74 | 45 | 58 | 326 | 241 | 670 |
| 75-100 | 76 | 129 | 978 | 529 | 1,712 |
| Total | 358 | 1,164 | 3,317 | 2,194 | 7,033 |

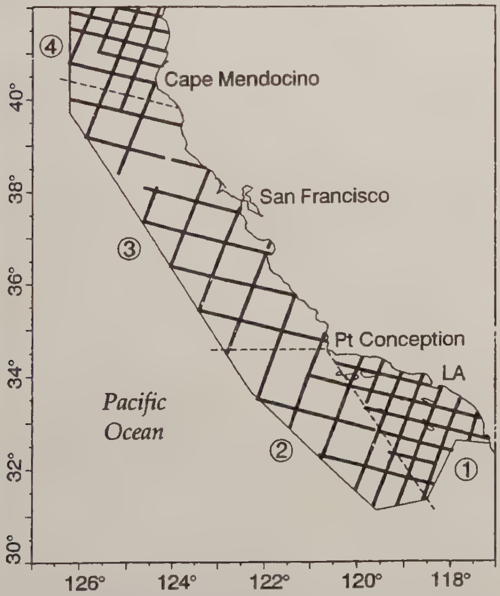

Fig. 3. Completed transects (solid lines) and *a posteriori* geographic strata (separated by dashed lines) used in the analysis. Area numbers are shown in circles.

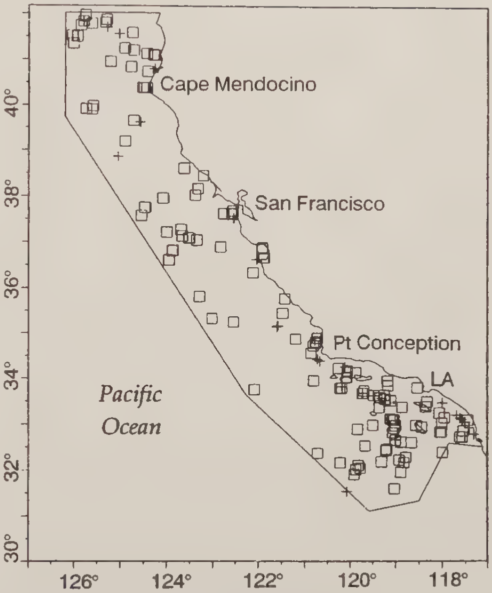

Fig. 4. Locations of all 155 cetacean sightings made during the survey. The 126 'on effort' sightings (used in the abundance estimation) are shown by squares, and the 29 'off effort' sightings (made while circling or in transit) are shown with plus signs.

Distributions of perpendicular distance from the trackline for individual species (based on both primary and secondary sightings) were combined into the three species/group size categories defined above (Analytical Methods section), based on similarities in the distributions. The Hazard model fit to the perpendicular distance distributions for each of the three categories is shown in Fig. 5. The probability of detecting a group of animals on the trackline, $g(0)$, was estimated separately for the three species/group size categories. Table 1 shows the assignment of individual species to the three groups, along with the estimates of $f(0)$ and $g(0)$.

Corrected and uncorrected abundance estimates along with estimates of precision are shown in Table 5. The chosen length of the sampling unit (5, 10, 15 or 20km) for the bootstrap simulation did not appear to influence the estimates of precision (Fig. 6), although for two species, the smallest segment length produced slightly different values than the other three. The percentile confidence limits and the CVs shown in Table 5 are taken from the bootstrap with a segment length of 20km.

## DISCUSSION

The estimates of abundance obtained from this survey are preliminary. They represent data from the first of two surveys which were designed to yield a combined level of

Table 3

Summary of on effort sighting information for all species seen by area. Survey effort is 1,862km for Area 1, 1,362km for Area 2, 2,552km for Area 3 and 1,290km for Area 4. Multi-species sightings are listed once for each species, so the totals are higher than the actual number of sightings.

| | No. of sightings by Area | | | | | Group size range | | No. of sightings by Area | | | | | Group size range |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | All | | | 1 | 2 | 3 | 4 | All | |
| Common dolphin (*D. delphis*) | 11 | 3 | - | - | 14 | 9-2,525 | Minke whale (*B. acutorostrata*) | 1 | - | 1 | 1 | 3 | 1 |
| Risso's dolphin (*G. griseus*) | 8 | 1 | 1 | - | 10 | 4-59 | Gray whale (*E. robustus*) | 7 | - | 6 | 2 | 15 | 1-10 |
| Pacific white-sided dolphin (*L. obliquidens*) | 2 | 2 | 3 | 1 | 8 | 1-848 | Humpback whale (*M. novaeangliae*) | - | - | 2 | 3 | 5 | 1-2 |
| Northern right whale dolphin (*L. borealis*) | 14 | 2 | 4 | 2 | 22 | 1-83 | Killer whale (*O. orca*) | - | 1 | - | 1 | 2 | 1 |
| Harbor porpoise (*P. phocoena*) | - | - | 7 | 5 | 12 | 1-2 | Sperm whale (*P. macrocephalus*) | - | - | 1 | - | 1 | 1 |
| Dall's porpoise (*P. dalli*) | 4 | 1 | 11 | 4 | 20 | 1-6 | Ziphiid whales | | | | | | |
| | | | | | | | *Mesoplodon* sp. | - | - | 1 | 1 | 2 | 1-2 |
| | | | | | | | *Z. cavirostris* | - | 1 | - | 1 | 2 | 1-5 |
| Bottlenose dolphin (*T. truncatus*) | 4 | - | 1 | - | 5 | 1-51 | Unid. Ziphiid | - | 1 | - | 1 | 2 | 1-2 |
| Unid. dolphin/porpoise | 3 | 3 | 4 | 1 | 11 | 1-9 | Unid. whale | 1 | 1 | 3 | 1 | 6 | 1-2 |
| **All small cetaceans:** | 46 | 12 | 31 | 13 | 102 | 1-2,525 | **All large cetaceans:** | 9 | 4 | 14 | 11 | 38 | 1-10 |

Table 4

List of unidentified sighting locations and assignment to individual species for the analysis. Assignment was selected from all species which could not be ruled out based on characteristics seen. See Fig. 2 for key to codes. In two cases, it was not possible to assign the sighting to a single species (see Results).

| Latitude | Longitude | No. animals | Code(s) | Assigned species |
|---|---|---|---|---|
| **Small Cetaceans** | | | | |
| 31°36.24'N | 118°59.65'W | 4 | DD/LO | *L. obliquidens* |
| 32°16.94'N | 118°44.93'W | 2 | WB/PD/TT | *P. dalli* |
| 32°39.63'N | 118°58.22'W | 1 | TT/SZ | *T. truncatus* |
| 32°06.05'N | 119°47.09'W | 6 | SD/PD | *L. obliquidens* |
| 33°57.13'N | 120°45.68'W | 1 | WB | *D. delphis* |
| 33°38.31'N | 119°12.92'W | 1 | SD | *D. delphis* |
| 36°20.16'N | 122°04.96'W | 1 | WB | *L. obliquidens* |
| 37°05.32'N | 123°29.94'W | 2 | SD/UP | *P. dalli* |
| 38°36.19'N | 123°35.73'W | 9 | SD | *L. obliquidens* |
| 39°58.25'N | 125°33.18'W | 8 | WB | *L. obliquidens* |
| 41°51.96'N | 125°15.15'W | 2 | LO/PD | *P. dalli* |
| **Large Cetaceans** | | | | |
| 31°57.84'N | 118°51.04'W | 2 | BB/BE/BP | *Balaenoptera* sp. |
| 31°54.71'N | 119°52.73'W | 1 | SZ/UK | Unid. Ziphiid |
| 34°52.49'N | 121°09.66'W | 1 | LW | *E. robustus* |
| 36°48.22'N | 123°50.91'W | 1 | LW | *M. novaeangliae* |
| 39°11.46'N | 124°51.43'W | 1 | UB | *M. novaeangliae* |
| 40°22.90'N | 124°24.18'W | 1 | LW | *E. robustus* |

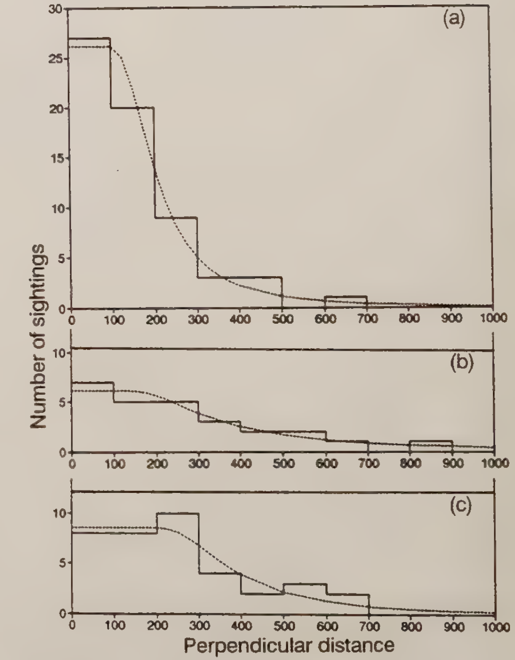

Fig. 5. Distribution of perpendicular sighting distances (100m intervals; solid line) and Hazard model fit (dotted line) for (A) small cetaceans in groups ≤10, (B) small cetaceans in groups >10, and (C) medium and large cetaceans.

precision in the abundance estimate corresponding roughly to a coefficient of variation of 0.36 for the common species. As expected, precision is lower than this after just one survey. However, these new abundance estimates are believed to be superior to other currently available estimates (Dohl *et al.*, 1978; 1983) for two reasons: (1) previous estimates do not include levels of precision; and (2) previous estimates are based on data which were collected over 10 years ago, and species distributions and abundances may have changed. For example, short-finned pilot whales, *Globicephala macrorhynchus*, which formerly were seen regularly along the California coast, were not sighted at all during this survey. Both of these factors introduce uncertainty which makes these previous estimates less useful for management purposes.

Although the variability in the presented estimates is quite large (CVs ranging from 0.28 to 1.07), it is likely to decrease considerably with data from the second survey,

Table 5

Uncorrected (U) and corrected (C) abundance estimates (N) for all cetacean species sighted during the 1991 aerial survey in California. Bootstrap estimates of precision are presented in terms of the 95% confidence limits and the coefficients of variation (CV) for the bootstrap simulations with segments of 20km length. The correction factor is assumed to be known without error.

| Species | | N | L95% | U95% | CV |
|---|---|---|---|---|---|
| *D. delphis* | U | 265,446 | 84,626 | 581,711 | 0.46 |
| | C | 277,783 | 88,837 | 608,516 | 0.46 |
| *G. griseus* | U | 9,807 | 3,109 | 23,564 | 0.49 |
| | C | 10,506 | 3,488 | 25,074 | 0.48 |
| *L. obliquidens* | U | 43,905 | 4,386 | 143,361 | 0.78 |
| | C | 46,334 | 5,228 | 150,241 | 0.78 |
| *L. borealis* | U | 11,820 | 5,130 | 26,659 | 0.43 |
| | C | 13,362 | 6,138 | 29,396 | 0.41 |
| *P. phocoena* | U | 1,014 | 290 | 2,092 | 0.45 |
| | C | 1,236 | 353 | 2,549 | 0.45 |
| *P. dalli* | U | 4,786 | 2,659 | 7,786 | 0.28 |
| | C | 5,832 | 3,240 | 9,487 | 0.28 |
| *T. truncatus* | U | 3,811 | 161 | 9,578 | 0.62 |
| | C | 4,011 | 196 | 10,038 | 0.62 |
| *B. acutorostrata* | U | 114 | 0 | 278 | 0.68 |
| | C | 117 | 0 | 285 | 0.68 |
| *E. robustus* | U | 1,680 | 507 | 3,324 | 0.42 |
| | C | 1,720 | 519 | 3,404 | 0.42 |
| *M. novaeangliae* | U | 395 | 110 | 776 | 0.42 |
| | C | 405 | 113 | 795 | 0.42 |
| *O. orca* | U | 85 | 0 | 222 | 0.76 |
| | C | 87 | 0 | 227 | 0.76 |
| *P. macrocephalus* | U | 55 | 0 | 210 | 1.07 |
| | C | 56 | 0 | 215 | 1.07 |
| Beaked whales | U | 493 | 147 | 1,017 | 0.44 |
| | C | 505 | 151 | 1,041 | 0.44 |
| Fin/Sei/Bryde's whale | U | 58 | 0 | 210 | 1.00 |
| | C | 59 | 0 | 215 | 1.00 |

particularly for the small cetaceans. The precision of estimates for some of the larger whales is expected to remain low due to the small numbers of sightings. However, abundance estimates for several species of the larger whales have been obtained with other, more efficient methods, such as photo-identification studies (blue and humpback whales: Calambokidis *et al.*, 1991) or land-based census techniques (gray whales: Reilly, 1984; Buckland, 1993).

Several sources of potential bias must be addressed. In this analysis, we have attempted to assess the magnitude of perception bias and correct for it in the abundance estimates. The estimated maximum proportion of animals missed ranges from 0.024 to 0.218 of all sightings, depending on group size and body size of the animals. If no other biases were occurring, the best point estimate would lie between the uncorrected and corrected values in Table 5. However, availability bias could not be corrected for in this analysis. This should produce a downward bias in the abundance estimate, whose magnitude will vary between species. The bias is expected to be smallest for species which tend to occur in large groups, and largest for species which spend relatively less time at the surface.

Although line transect methods are robust to pooling different distributions (Burnham *et al.*, 1980), the pooling of all environmental conditions is likely to introduce a downward bias in the abundance estimation due to the lower probability of sighting animals on the trackline under poor conditions (Holt, 1987; Barlow *et al.*, 1988; Forney *et al.*, 1991). The magnitude of this bias is unknown, and is likely to vary between species. Our method of correcting for missed groups may account for some of this bias, but may not be robust to heterogeneity in the fraction missed due to environmental conditions.

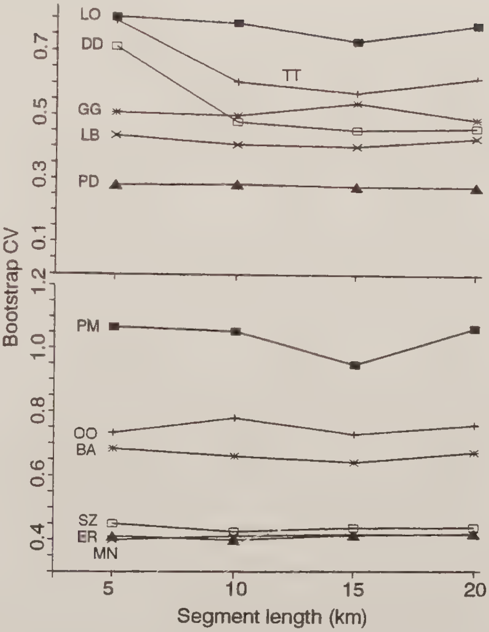

Fig. 6. Coefficients of variation (based on 1,000 replicates) for simulations using bootstrap segment lengths of 5km, 10km, 15km and 20km. See Fig. 2 for key to species codes.

Potential upward bias in line transect analysis can result if factors other than distance to the trackline affect the probability of seeing a school. School size has been shown to affect the probability of detection (Drummer, 1985; Holt and Sexton, 1989), and this can lead to an upward bias in the abundance estimate (Quinn, 1985; Drummer and McDonald, 1987). To counteract this effect, we have stratified small cetacean sightings by group size and estimated abundances separately for small and large groups of the same species. This is an artificial separation, but it reduces potential biases due to large variation in group size within a single species.

In summary, three sources of downward bias and one source of upward bias in the abundance estimates have been identified. We have corrected for one of the sources of downward bias (perception bias), and attempted to minimise the upward bias by a post-stratification by school size range. Overall, our estimates may still be biased downward.

When comparing the current abundance estimates with those made previously by other researchers, the differences vary between species. Estimates for Pacific white-sided dolphins and Dall's porpoise, for example, are similar to previous values of approximately 26,000–86,000 and 3,000–9,000, respectively (Dohl *et al.*, 1978; 1983). The corrected estimate of 405 humpback whales is also similar to recent estimates based on photo-identification work (Calambokidis *et al.*, 1991), despite differences in seasonal timing of these studies. Other species previously recorded were not seen at all during this aerial survey (e.g. short-finned pilot whales) and some were seen in greater numbers than before. The most notable disagreement is for common dolphins, with the current corrected winter estimate (277,783) being more than an order of magnitude larger than the previous value of 15,488 (CV=0.36; Dohl *et al.*, 1986). The validity of the new estimate is supported by the 1991 summer/fall estimate from a ship survey, which is also in the hundreds of thousands of animals (Barlow, 1993).

Two of the species for which abundance estimates were made occur in two distinct forms in California waters. The two forms of common dolphins (offshore and neritic) are currently undergoing a taxonomic review and may be divided into two distinct species (Heyning and Perrin, 1991; Rosel, 1992; Dizon *et al.*, In press). Although clear differences in color pattern, size and beak length exist between these two forms, it is not always possible to differentiate them from the air, and the abundance estimate here is a combined estimate. If future assessments require separate estimates for the two forms, aerial surveys may not be adequate.

The second species which occurs in two forms is the bottlenose dolphin, which is divided into a coastal population found very close to shore along portions of the California mainland (Hansen, 1990; Maldini, 1991), and an offshore population, which is distributed more widely in offshore waters (Hansen, 1990). All of the animals seen during this survey were at least several miles from the mainland, so the estimate presented here is assumed to represent the population of offshore animals. Separate aerial surveys are currently being conducted by NMFS to assess year-round abundance of the coastal bottlenose dolphin.

Estimates for harbor porpoise and gray whales are substantially lower than previous estimates (Reilly, 1984; Barlow, 1988; Barlow *et al.*, 1988; Buckland, 1993). This is likely to be due to the fact that the defined study area is not appropriate for the range of these animals. Gray whales have a much larger range and migrate through California waters (southward and then northward) from roughly November to May. The current estimate can be thought of as that portion of the population which was migrating through California in March and early April. Harbor porpoise are limited to a narrow coastal band, and our tracklines only overlapped with this region at specific points. The overall sighting rates are therefore not representative of the total area in which harbor porpoise occur.

The estimates presented for the beaked whales as a group can be viewed as a combined estimate for whales of the genus *Mesoplodon* and *Ziphius cavirostris*. All unidentified beaked whale sightings could be narrowed down to these two genera. The only other beaked whale species known to occur in this region, *Berardius bairdii*, can be readily distinguished based on its size and was not sighted during this survey.

In summary, although we were not able to complete the two full survey grids as planned, sightings were sufficient for most of the small cetacean species and for the beaked whales as a group to obtain reasonable estimates with confidence limits. The analysis indicates that precision is likely to reach acceptable levels when data from the 1992 aerial survey are included. Coupled with the summer/fall ship survey estimates, these studies will provide valuable insights into seasonal changes in distribution of cetaceans along the California coast, as well as potential historical changes. Given the uncertainty in abundance estimates, we stress the importance of presenting confidence limits. Bootstrap percentile confidence limits may be improved upon in the future with more advanced bootstrap procedures (Efron, 1987). Sensitivity of the estimates to our method of assigning 'unknown' sightings to species also requires examination. Furthermore, surveys must be designed with a target level of precision in mind to ensure that an appropriate level of survey effort is completed.

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*Toxic Phytoplankton Blooms in the Sea*
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# GLOBAL CLIMATE CHANGE AND HARMFUL ALGAL BLOOMS: THE EXAMPLE OF *Gymnodinium catenatum* ON THE GALICIAN COAST

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## ABSTRACT

A scenario is presented in which the incidence of blooms of the toxic dinoflagellate *Gymnodinium catenatum* on the coast of Galicia (NW Spain) could increase due to global climate change. Blooms of *G. catenatum* in the Galician rias appear to be related to the autumn relaxation of upwelling. This results in the incursion of warm, nutrient-depleted surface water into the rias, deepening the nutricline. Being a chain-former, *G. catenatum* is an effective swimmer and better adapted to vertical migration than other dinoflagellates. Thus, a deepening of the nutricline may favor this species which is capable of migrating to the deep layers to take up nutrients. It is expected that atmospheric "greenhouse" effects will intensify equatorward wind stress along the west coast of the Iberian Peninsula during spring and summer, thereby amplifying coastal upwelling. This would increase the temperature difference between recently upwelled waters and surface waters of oceanic origin, and enhance primary production and mussel growth within the rias during summer. The estuarine circulation of the rias would then export increased particulate organic matter (phytoplankton and mussel feces) from the rias. This organic matter would tend to settle and remineralize on the continental shelf near the mouth of the rias, increasing the nutrient concentration of the waters entering the rias below the nutricline. The combination, during fall, of increased nutrient concentrations below a deepened nutricline and a more strongly stratified water column would seem to be particularly favorable to *G. catenatum*. The first recorded observation of this species was in 1976 when the first PSP outbreak associated with Galician bivalves was also reported. Conversely, *Gonyaulax polyedra*, a common bloom species in the past, is now rare in the rias.

## INTRODUCTION

Recent decades have seen a continuing build-up of $CO_2$, methane, chlorofluorocarbons, and other greenhouse gases in the earth's atmosphere. The scientific consensus is that substantial global warming and other important climatic effects are likely [1]. There is growing concern that associated changes in the coupled atmosphere-ocean system, brought about by this accumulation, may have major effects on marine ecosystems, their living resources and associated human cultural and economic values. One "greenhouse effect" which seems certain is an increase in temperature contrast between the heated continental land masses and the oceans during the warmer seasons of the year. This would lead to amplified sea breeze circulations and alongshore coastal winds, correspondingly enhanced offshore Ekman transport in the ocean surface layer, and intensified coastal upwelling [2].

Another important global trend related to human activities is the increased economic and public health problems related to harmful algal bloom phenomena [3]. Although these trends have not been linked mechanistically, the potential for linkage of global climate change to the harmful bloom problem is certainly of great interest.

The ocean adjacent to the west coast of the Iberian Peninsula is a "classic" eastern ocean coastal upwelling system. The upwelling process is highly seasonal, being most intense in spring and summer, but relaxing during fall and winter [4]. Nutrient-rich, upwelled waters provide a basis for high rates of organic production, a rich trophic pyramid and important local fisheries. Major mariculture operations occur in the Rias Bajas, a series of oceanic bays on the coast of Galicia (Fig. 1), where intermittent enrichment during upwelling events supports intensive raft culture of mussels [5]. The toxic dinoflagellate *Gymnodinium catenatum* Graham was first observed in October, 1976, coinciding with the first recorded outbreak of paralytic shellfish poisoning (PSP) in Spain [6]. Over the past decade, PSP outbreaks have become a serious threat to the local mariculture industry.

This paper utilizes recent advances in understanding the ecology of chain-forming dinoflagellates, such as *G. catenatum*, and the likely effects of global climate change on coastal upwelling ecosystems, such as the Galician Coast, to provide an example of a credible scenario for linkage of global climate change and harmful algal bloom phenomena. The goal is to stimulate discussion and motivate interdisciplinary research activity on a topic of potentially serious socio-economic and public health concern.

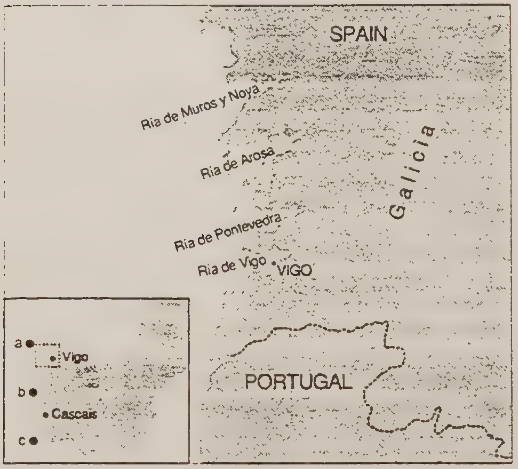


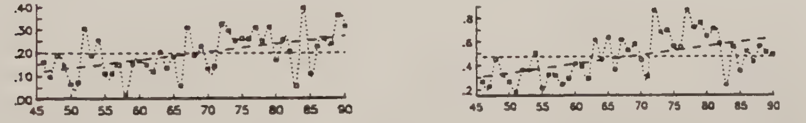
FIG. 1: The Iberian Peninsula, with locations referred to in text and detail of the Rias Bajas region.

## CLIMATE CHANGE AND UPWELLING ECOSYSTEMS

Eastern ocean upwelling ecosystems are the most productive, extensive ocean areas of the world. In such regions, equatorward alongshore winds cause offshore transport in the surface Ekman layer. This loss of surface water near the coast is balanced by upwelling of cool, nutrient-rich waters from depth. During active upwelling, the offshore surface Ekman flux maintains a slight sea surface slope implied by the density difference between the upwelled water near the coast and the lighter surface waters a short distance offshore. However, during relaxations or reversals in upwelling-producing wind stress, the lighter oceanic surface water tends to collapse coastward [7], overrides the newly upwelled water, and downwells at the coast. Downwelling has been observed to extend to within the Rias Bajas, following the initial seasonal relaxation of upwelling along the Galician coast [8].

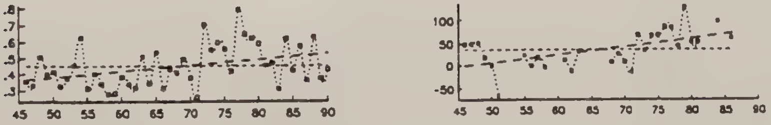
The vigorous alongshore wind that drives the upwelling is supported in part by a strong atmospheric pressure gradient between a thermal low pressure cell that develops over the heated land mass and the higher barometric pressure offshore over the cooler ocean. This is one reason why upwelling seasons tend to encompass nearly the entire year in tropical eastern ocean boundary systems but, with increasing latitude are more restricted to a late spring to summer period [4]. Greenhouse-related amplification of heating during spring and summer would intensify the thermal low pressure cell, enhancing the onshore-offshore pressure gradient. The stronger pressure gradient would strengthen the alongshore geostrophic wind, causing enhanced offshore Ekman transport and amplified coastal upwelling. The increased upwelling and mixing implied by such a wind increase, by cooling the coastal ocean surface layers and further accentuating the ocean-continent temperature contrast, might constitute a positive feedback loop [2] further amplifying the effect.

Eastern sides of oceans have a much drier atmosphere than western sides. Since the most important greenhouse gas in the atmosphere is water vapor, the global accumulation of $CO_2$, methane, chlorofluorocarbons, etc., will have a larger relative greenhouse effect along eastern ocean boundaries than in other ocean regions. Thus, one would expect the effect to emerge from the "noise level" of natural, short term climatic variability earlier in these regions than elsewhere. However, since the effect on the wind system is to increase upwelling and mixing (both of which cool the sea surface), it is not surprising that general increases in average sea surface temperature have not been an evident consequence in these systems. On the other hand, the intensity of upwelling-producing wind stress (Fig. 2) off the Iberian Peninsula has appeared to increase dramatically during spring and summer over the past four decades [2, 9, 10]. During this period, a sustained increase in spring-summer alongshore sea level slope (relative to fall-winter) (Fig. 2d) tends to corroborate this trend. These and various other aspects of the seasonality and geography of wind stress trends throughout the North Atlantic conform well to a greenhouse effects scenario [10].



a. North

b. Central



c. South

d. Sea Level Slope

FIG. 2: Long term (1946-1990), increasing trends in upwelling-producing wind stress and alongshore sea level slope (after [10]). Panels a, b, c: spring-summer (April to September) average monthly wind stress (dyne $cm^{-2}$) for three locations (a, b, c) off the Iberian coast (see FIG. 1). Long-term mean for each series indicated by horizontal, dashed line. Linear trend lines fitted by least squares. Panel d: seasonal (spring-summer minus fall-winter) difference in sea level slope (in mm) between Cascais and (minus) Vigo (see FIG. 1).

## ECOLOGY OF *Gymnodinium catenatum* IN THE RIAS BAJAS

In a study of nutrient dynamics within the rias, Fraga [11] provided the scenario diagrammed in Figure 3: "In spring the upper levels of the NACW (North Atlantic Central Water) rise above the level of the bottom of the Rias, and nutrient-rich water reaches the photosynthetic layer inside the rias leading to high primary production. Part of the biomass produced is transported in the surface layer towards the mouth of the rias, sinks to the bottom, and decomposes. This enriches the deep water, which flows back into the rias." A relationship exists between mussel production within the rias and intensity of coastal upwelling outside the rias [12], based on a comparison of a mussel-condition index (% solids) and an upwelling index [13] computed from the atmospheric pressure gradient at a point 150 km off Cape Finisterre. Thus, the amount of particulate solids involved in the transport, sinking, decomposition, and remineralization loop (Fig. 3) would tend to increase with upwelling intensity.

*G. catenatum* blooms in the Galician Rias have been associated with the autumn relaxation of the summer upwelling [14, 15]. In late summer, sea surface temperatures in the rias are relatively cool due to the influence of coastal upwelling. Offshore, warm and salty water related to a coastal current [16] occurs at the surface. When the prevailing southward winds, which drive summer upwelling, relax or turn northward in the fall, the surface waters held offshore by the wind-induced offshore Ekman flux collapse toward the coast causing downwelling in the rias. Phytoplankton dominance then changes from diatoms to dinoflagellates. *G. catenatum* is one of the dinoflagellate species that may bloom at this time (see Fig. 2 in [17] ). When this occurs, mussels may become toxic to humans [14].

Vertical migration is an important factor in dinoflagellate blooms. *G. catenatum*, as observed during a bloom in the Ria de Vigo in 1986 [8], is able to undertake daily vertical migrations to transport nutrients from the deep nutricline to the illuminated surface layers for use in photosynthesis. In Galicia, *G. catenatum* commonly blooms together with *Alexandrium affine* in areas of downwelling, inside or near the mouths of the rias. These two species and other "red tide" dinoflagellate species can form long chains. Fraga *et al.* [18] reported that the swimming speed increases with chain length. This apparent hydrodynamical advantage results in the chain-forming dinoflagellates being better adapted for vertical migration than single-celled forms. (We diagram this "fall" scenario in Fig. 4). The advantage may be substantial when significant downwelling is occurring and/or the nutricline is deep. Thus, the depth of the nutricline appears to be a selection factor for chain-forming species over single-celled dinoflagellates or non-motile phytoplankters such as diatoms.

## A SCENARIO LINKING CLIMATE CHANGE TO TOXIC BLOOMS

The following "linkage scenario" is accordingly proposed. If climate change leads to increased upwelling intensity, the input of nutrients and primary production in the rias will increase during the upwelling season (April - September). The production of particulate organic matter, notably increased fecal matter from increasingly well-nourished mussel culture, will also increase and enter the transport, sinking, decomposition, and remineralization "loop" (Fig. 3). This would result in a greater accumulation of decaying organic matter on the bottom. Subsequent remineralization would increase nutrient concentrations in the layer beneath the deep nutricline following the upwelling season (Fig. 4). Vertically-migrating, chain-forming phytoplankters, such as *G. catenatum*, would have the best access to this increased deep nutrient pool.

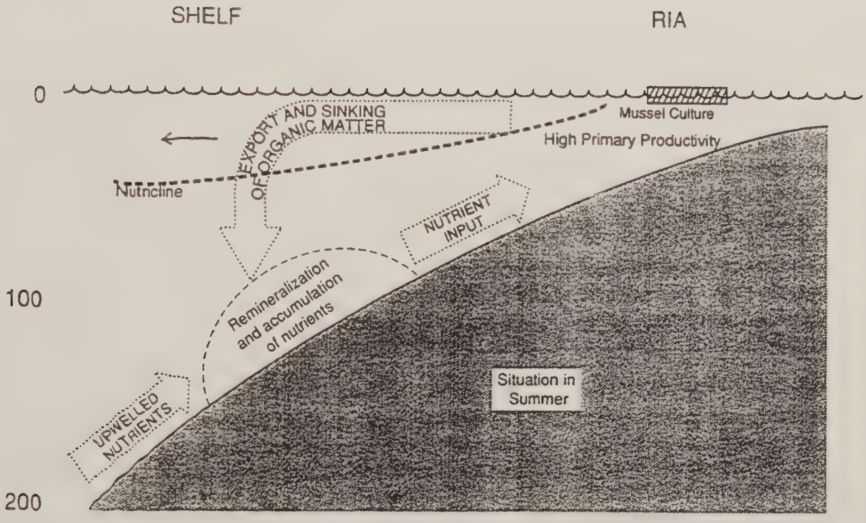

SHELF
RIA
0
100
200
EXPORT AND SINKING OF ORGANIC MATTER
Mussel Culture
High Primary Productivity
Nutricline
NUTRIENT INPUT
Remineralization and accumulation of nutrients
UPWELLED NUTRIENTS
Situation in Summer

FIG. 3: Diagram of summer nutrient dynamics in the rias and adjacent continental shelf illustrating the "loop" consisting of upwelling-enriched primary production, which leads to export, sinking, and bottom accumulation of particulate organic matter, which decays, remineralizes, and enriches waters beneath the nutricline which may be resupplied to the photic zone by subsequent upwelling.

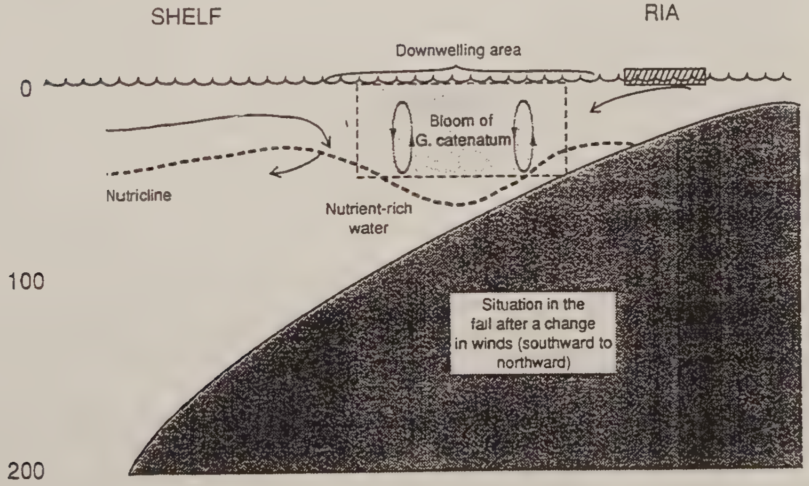

SHELF
RIA
Downwelling area
0
100
200
Bloom of G. catenatum
Nutricline
Nutrient-rich water
Situation in the fall after a change in winds (southward to northward)

FIG. 4: Diagram of nutrient dynamics after fall relaxation of upwelling. Lighter oceanic surface waters collapse toward the coast producing a downwelling zone in the rias which cuts off upwelled enrichment of the photic zone and depresses the nutricline. Vertically-migrating dinoflagellates may access the nutrient pool beneath the nutricline and transport assimilated nutrients to the photic zone for use in photosynthesis.

In addition, an increased upwelling intensity would be expected to increase the equatorward sea surface slope along the Iberian Peninsula. Thus, the initial collapse of the offshore surface water towards the coast upon cessation of the upwelling wind would tend to be intensified. (An increased southward, alongshore sea surface slope would increase the tendency for coastward geostrophic flow and tend to break down (by opposing southward momentum) maintenance of the offshore sea surface slope by Coriolis force, which holds the lighter oceanic surface waters offshore). This would enhance the episodic, fall downwelling within the rias and deepen the nutricline, favoring forms such as *G. catenatum* which are adapted for vertical migration.

As noted above, there is evidence that both upwelling intensity and seasonal (upwelling vs. non-upwelling) differences in sea level slope are indeed increasing along the Iberian coast and in other eastern ocean boundary regions. An apparent change in bloom species has also been observed [19] in the Rias Bajas. The first known reports of "red tides" in Galicia are from 1916 and 1917 [20], with the next report from 1955 [21]. In these three earlier blooms, *Gonyaulax polyedra* was the main species, but is now rare in these waters. In fact, several species which now form "red tides" in the rias (*G. catenatum*, *A. affine*, *Prorocentrum triestinum*, *Heterosigma akashiwo*) were not reported before the last decade. The hypothesis that these species represent recent introductions has been popular, given the introduction of viable dinoflagellate resting cysts into Tasmanian waters from the ballast waters of large cargo ships [22]. Admittedly, climate change is not the only potential explanation. The environment within the rias has been subjected to substantial alterations within this century. The human population inhabiting the shores of the rias has increased dramatically and mussel culture, initiated in the 1950s, has substantially altered nutrient dynamics in the rias.

Although aspects of this proposed scenario linking toxic bloom phenomena to global climate change are speculative, it represents a logical sequence of reasonably likely circumstances. The possibility emerges that an affect on harmful algal bloom phenomena may be one of the most direct consequences of climate change with regard to impacts on marine ecosystems and associated human values. There presently seems to be a nearly total absence of focus on this problem area within the various national or international global climate change research programs. It would, therefore, seem prudent to seek ways to encourage the design and implementation of expanded research activities in this area.

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# WILDLIFE SOFTWARE

## TRENDS: SOFTWARE FOR A POWER ANALYSIS OF LINEAR REGRESSION

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Linear regression often is used in wildlife studies to assess trends. A typical use would be to assess growth or decline in population size over time. However, before commencing a program to monitor populations, several questions should be considered: (1) how many years should monitoring continue to detect a change; (2) how precise must an index be; (3) how large a change can be detected; and (4) what is the probability of detecting a change (obtaining a significant slope to the regression line), given that a change really is occurring?

Posing such questions is fundamental to a well-designed monitoring program. Obtaining answers through a statistical power analysis is important during both the design and analysis stages of a study. Tables (Cohen 1988) and microcomputer software (Goldstein 1989) are available to perform power analyses for many common statistical tests. We developed power analysis software for linear regression (program TRENDS) while designing surveys for dolphins (*Stenella* spp.) in the eastern tropical Pacific Ocean (Gerrodette 1987, 1991; Holt et al. 1987). TRENDS will be useful to biologists designing field studies, but it also could be used by teachers and students in courses on experimental design and statistics.

TRENDS is simple to use and parametrizes the problem in easily understood terms. It can be applied in any situation where linear regression analysis is appropriate, and where estimates of the dependent variable are made at equal (or nearly equal) intervals. Thus, the program is not limited to detecting trends in a time series of population size, but could be applied generally to any variable of interest measured at equal intervals. The program is a single file (TRENDS.EXE) executable on any IBM-compatible microcomputer. Input and output are via ASCII files created by the program; no graphics are produced. Source code is Microsoft FORTRAN 77.

TRENDS summarizes the power analysis in 5 parameters: (1) $n$, the number of sampling occasions (points in the regression); (2) $r$, the rate of change between each sampling occasion (slope of the regression line); (3) $CV1$, the coefficient of variation (ratio of standard deviation to mean, a measure of precision of estimation on each sampling occasion); (4) $\alpha$, the significance level (probability of a Type 1 error); and (5) power ($1 - \beta$, where $\beta$ is the probability of a Type 2 error). The value of any parameter can be estimated if the other 4 are specified. The parameter of interest depends on the particular application.

The relationships among these parameters are affected by several other factors: (1) whether change is linear or exponential, (2) whether change is positive or negative, (3) whether the statistical test is 1- or 2-sided, (4) how the precision of the estimates depends on abundance, and (5) which statistical distribution is used. The latter 2 factors depend on the method used to estimate abundance (line-transect surveys, mark–recapture methods, etc.) and the error structure of the estimates. TRENDS allows the user to choose among several possibilities.

The following example of the use of TRENDS is based on data presented in Storm et al. (1992). They found a mark–resight method superior to an area-conversion method for estimating white-tailed deer (*Odocoileus virginianus*) density, and stated that "we expect to continue monitoring the herd size during the next 5 years" (Storm et al. 1992:201). Is the mark–resight method also superior to the area-conversion method for monitoring herd size? What trends in population size can we expect to detect in 5 years? Using data presented in Storm et al.'s (1992) Table 2, we can estimate that, with 90% power over a 5-year period at a significance level of $\alpha = 0.05$, the minimum detectable annual rate of growth is 25% with the mark–resight method and 27% with the area-conversion method (see the user's guide for details). Lower rates of growth have a <90% chance of being detected in 5 years. Reformulating the problem to estimate the probability of detecting a 10%/year rate of herd size growth over a 5-year period yields detection probabilities (power) of 0.41 for the mark–resight method and 0.29 for the area-conversion method. These answers are approximate, but they indicate that mark–resight provides a slightly more sensitive method of monitoring deer herd size than area-conversion. Neither method, however, provides reasonable assurance of detecting a trend of 10%/year in 5 years. To detect such a trend with higher probability, we must expend more effort each year so that the herd size estimate has a smaller standard error, or we must continue monitoring for a longer period of time.

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# SURVIVAL RATES FOR THE HAWAIIAN MONK SEAL (*MONACHUS SCHAUINSLANDI*)

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## Abstract

Endangered Hawaiian monk seal (*Monachus schauinslandi*) pups at all the major breeding islands in the Northwestern Hawaiian Islands have been tagged since the early 1980s. Pups were double flipper tagged as soon as possible postweaning. With few exceptions, an extensive tag resighting effort was conducted annually at the same islands. These resighting data were used to estimate seal survival rates from the time of tagging to age one at all locations using the ratio of seals alive in the second year to number of pups tagged. These survival rates among the islands, from weaning to age one, averaged over the years of the study, ranged from 0.80 to 0.90. For young seals over age one, capture-recapture methods were used to calculate survival pooled through several years, and these rates ranged from 0.85 to 0.98. At French Frigate Shoals and Laysan Island, the higher numbers of tagged pups allowed separate estimates of male and female survival to be calculated. These rates suggested that survival of immature females was better than males. Beginning in 1989, survival of immature seals at French Frigate Shoals declined sharply.

Key words: Hawaiian monk seal, *Monachus schauinslandi,* survival, tag resighting, Jolly-Seber.

The Hawaiian monk seal population has declined substantially in numbers since the first reliable range-wide counts were made in the late 1950s (Rice 1960; Johnson *et al.* 1982; NMFS, unpublished data). Concern over this decline led to the species being listed as endangered under the U.S. Endangered Species Act in 1976. In order to assess possible causes of the decrease, monitor the status of the population, and evaluate the efficacy of recovery actions, tagging of weaned pups was initiated on Kure Atoll in 1981 (Gilmartin *et al.* 1986), Lisianski Island in 1982 (Henderson and Johanos 1988), and then expanded to all other major breeding islands by 1984. Pup tagging and intensive resighting

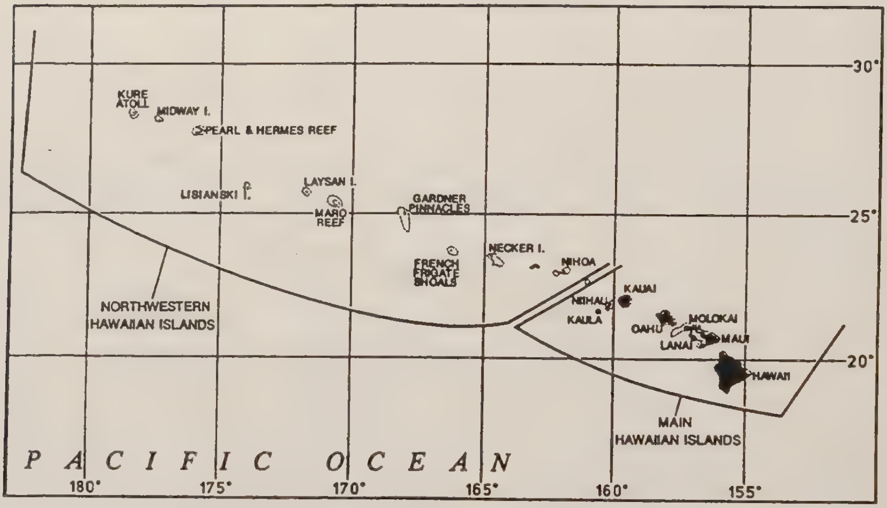
KURE ATOLL
MIDWAY I.
PEARL & HERMES REEF
LISIANSKI
LAYSAN I.
MARO REEF
GARDNER PINNACLES
NECKER I.
FRENCH FRIGATE SHOALS
NIHOA
NIIHAU
KAUAI
KAULA
OAHU
MOLOKAI
LANAI
MAUI
HAWAII
NORTHWESTERN HAWAIIAN ISLANDS
MAIN HAWAIIAN ISLANDS
PACIFIC OCEAN
30°
25°
20°
180°
175°
170°
165°
160°
155°

*Figure 1.* Hawaiian Archipelago.

efforts have involved long visits to most of the sites in subsequent years, resulting in resighting of a high fraction of the surviving tagged individuals. Assessment of survival from birth to weaning for the Hawaiian monk seal has been based on counts of dead pups of preweaning age recovered annually from the breeding islands. These data show preweaning survival among the breeding sites to be approximately 93% (NMFS, unpublished data).

The present paper reports survival rates among the five major monk seal breeding locations at Kure Atoll, Pearl and Hermes Reef, Lisianski and Laysan Islands, and French Frigate Shoals (Fig. 1) determined from the resighting data of pups tagged post-weaning.

## METHODS

*Pup tagging*—Beginning in 1981, weaned Hawaiian monk seal pups were tagged with colored and engraved plastic Temple Tags® between the fourth and fifth digit of each rear flipper as described by Gilmartin *et al.* (1986). A study to evaluate the effects of tagging weaned pups was conducted on Lisianski Island in 1982 utilizing a control group of weaned pups that were only marked with identifying numbers applied to the pelage with a commercial hair bleach when the seals were sleeping (Henderson and Johanos 1988). Results of this pilot study did not indicate significant differences between the tagged and control groups and enabled the pup tagging effort to be conducted at all breeding locations in subsequent years. Pups are double-tagged and lost tags are replaced soon after one tag is observed missing. Identities of seals based on photographs of scars and natural markings are also annually updated and cataloged. The latter effort provides a means of individual identification should both flipper tags be lost at the same time and assures that tag loss is of minor importance.

No tagging or resighting effort occurred at Lisianski Island in 1989, and abbreviated visits were necessary at Lisianski Island in 1988 and Pearl and Hermes Reef in 1990, reducing the number of pups tagged and the resighting effort for those years.

*Estimation of survival rates*—Although high annual resighting rates of tagged individuals were common, a few individuals were not seen in some intervening years, and others were identified at sites other than those at which they were tagged initially. Therefore, the most general capture-recapture model, the Jolly-Seber method (Seber 1982), was used for parts of the study. However, in most instances the very high resighting rates and fidelity to birth sites facilitated the use of much simpler estimation models, described by Haldane (1955) and Chapman and Robson (1960).

Even though nearly all of the weaned pups were tagged in most years, the low number of pups born annually at sites other than French Frigate Shoals resulted in small numbers being available for tagging, thus males and females were combined for many of the analyses. The small numbers also made it advantageous to use the simplest survival model available.

The simple model used here assumes a constant annual survival rate, and can be written as:

$$n_x = ps^x N \qquad (1)$$

where $N$ is the initial number tagged, $s$ is annual survival rate, $p$ is proportion of those present actually resighted in a given year, and $n_x$ is the number resighted in year $x$. Haldane (1955) used a similar geometric model but considered the numbers of tagged individuals dying in each year. Chapman and Robson (1960) gave an extensive analysis of the geometric distribution for use in estimating survival rates from a "catch curve"; *i.e.*, numbers of individuals of successive ages in a sample. Seber (1982: Sec. 5.4) gives a general model for tag recoveries from dead animals.

If one takes the natural logarithm of Equation 1, a linear equation results:

$$\log_e n_x = \log_e(pN) + x \log_e s, \qquad (2)$$

and this can be fitted by ordinary regression methods. This approach is not as satisfactory as methods based on Equation 1 because using Equation 2 on results of a tagging study is not likely to conform to the normal theory model for linear regression (Chapman and Robson 1960). However, some of the data of this study has missing years and years of low resighting rates, so the regression model is useful for provisional analyses of such data because these years can be excluded in the regression model.

Chapman and Robson (1960) gave an equation for the maximum likelihood estimator for a sequence of observations from a geometric distribution:

$$\frac{T}{n} = \frac{s}{1-s} - \frac{(k+1)s^{k+1}}{1-s^{k+1}}; \qquad (3)$$

where $k$ denotes the number of successive observations beyond the first used, $n = n_0 + n_1 + n_2 + \ldots + n_k$, where $n_i$ is the number of individuals observed on the $i$th occasion, and $T = n_1 + 2n_2 + \ldots + kn_k$. This equation must be solved by iteration.

Haldane (1955) considered the situation where several such sequences were combined. Using the notation above, his equation becomes:

$$\Sigma \left\{ \frac{T_j}{n_j} - \left[ \frac{s}{1-s} - \frac{(k_j+1)s^{k_j+1}}{1-s^{k_j+1}} \right] \right\} = 0; \tag{4}$$

with the variance estimate:

$$Var(s) = \left[ \Sigma \left\{ \frac{n_j}{s(1-s)^2} - \frac{(k_j+1)^2 s^{k_j-1} n}{(1-s^{k_j+1})^2} \right\} \right]^{-1}. \tag{5}$$

It should be noted that the above methods all assume that both $p$ and $s$ are constant throughout.

First-year survival rates were estimated differently. Long visits to each site and frequent observations resulted in very high resighting rates in most instances. Occasionally, an individual was not observed in a given year, but survivors were almost always seen in the second year. Consequently, "back-corrections" could be used after an interval of two or three years, and first-year survival calculated as the ratio of numbers alive in the second year over number of weaned pups tagged. For consistency, and to be virtually certain of the back-calculations, we based first-year survival estimates on data for cohorts tagged through 1987.

Pollock *et al.* (1990) note that estimates of the kind used here to calculate first-year survival may be subject to a negative bias. This possibility was evaluated by using equation 5.2 of Pollock *et al.* (1990) along with an equation for the probability that an individual will be sighted again given by Lebreton *et al.* (1992). Jolly-Seber calculations for sites other than Kure (where survival is very high and potential bias negligible) gave an average probability of sighting ($P$) of 0.98 at sites other than Pearl and Hermes Reef, where it averaged 0.95. Assuming a first-year survival rate of 0.8 and subsequent annual survival rates of 0.9, the bias was less than one percentage point of survival, and thus was neglected.

A Kure Atoll recovery project (Gerrodette and Gilmartin 1990) involved collection and rehabilitation of some emaciated female pups from French Frigate Shoals and release of them at Kure, so the first-year survival at French Frigate Shoals is based on the number of tagged pups less those removed for rehabilitation (listed separately in Table 1).

*The Jolly-Seber method*—The general Jolly-Seber method is discussed in detail by Seber (1982: chapter 5). In this form the method utilizes repeated releases of newly tagged individuals, along with those animals caught on the $i$th capture occasion that had been tagged previously. Seber denotes these releases of previously and newly tagged animals as $R_i$, while previously tagged animals caught on the $i$th occasion are denoted as $m_i$. Inasmuch as there was no tagging after the first release of a tagged cohort in the present context, we have $R_i = m_i$. Two other quantities needed here are $r_i$, the number of tagged individuals caught later of those ($R_i$) released on the $i$th occasion, and $z_i$, the number of individuals tagged before the $i$th sampling occasion and caught after that occasion but not caught on the $i$th occasion. With this notation, the estimate of survival from occasion $i$ to occasion $i + 1$ (Seber 1982: equation 5.9) becomes:

$$\hat{\Phi}_i = \frac{m_{i+1}\left(\frac{z_{i+1}}{r_{i+1}} + 1\right)}{m_i\left(\frac{z_i}{r_i} + 1\right)}. \tag{6}$$

Because a very high fraction of tagged animals are seen each year, the $z_i$ are frequently zero (or very small), so the survival estimates by this equation reduce largely to the ratio of tagged individuals resighted in two successive years. With relatively small samples such ratios will be highly variable so Equation 6 is only used for the largest samples here. However, the Jolly-Seber calculations were conducted on data from all sites other than Kure, to provide estimates of the probability of sighting to check on the bias in estimating first-year survival described by Pollock *et al.* (1990).

*Variance of survival estimates*—Because the present application of the method of Haldane (1955) is based on repeated observations of the same individuals, it seemed worthwhile to check the variance estimate of Equation 5. This was done with a monte carlo simulation with 30 tagged seals in each of 6 cohorts, survival of 0.90, annual sighting probability of 0.95, and runs of 1,000 simulations. The outcomes gave survival estimates very close to 0.90, but 95% confidence limits were appreciably too wide ("coverage" of about 99.9%) while percentile confidence limits from bootstrapping (Efron and Gong 1983) in the simulations were close to 95%. Consequently, bootstrapping confidence limits (B.C.L.) are given here for all estimates, with the exception of data from Kure Atoll, where convergence problems in the bootstrapping led to use of Equation 5.

## RESULTS

A summary of the tagging and resighting data appears in Table 1, and the analyses are discussed by individual sites below:

*Kure Atoll*—Kure sample sizes are small, but survival rates were 100% for tagged cohorts over long time periods (Table 1), and only in two instances was a tagged individual not seen in one year, then seen later. Using the ratio of one-year-olds to those tagged as weaned pups from 1981 through 1987 gave a first-year survival of 28/32 = 0.88. Pooling all of the Kure Atoll sighting data from the first resighting onwards gave an overall survival rate Equation 4 of 0.98 (0.03). The standard error from Equation 5 is given in parentheses after the estimate. Clearly, the main losses observed at Kure Atoll were in the first year after tagging. The Kure Atoll data in Table 1 are from Kure-born seals only. However, rehabilitated yearlings placed at Kure have also shown good survival after release.

*Pearl and Hermes Reef*—This site is difficult to survey adequately for tag resightings because the atoll contains many small islets scattered along the fringing reef on which monk seals haul out and can be easily disturbed by an observer.

*Table 1.* Resighting data for Hawaiian monk seals tagged as weaned pups on major sites. KUR = Kure Atoll, PHR = Pearl and Hermes Reef, LIS = Lisianski, LAY = Laysan, and FFS = French Frigate Shoals. The tag resighting effort was low in some years.[a] Some undersized weaned pups were removed from the population for rehabilitation and eventual release or for permanent captivity.[b] The table excludes survival data from these seals, however, the total number tagged, including these seals, is shown in parentheses.

| Island | Year | Sex | No. tagged | Number seen in year *X* | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| KUR | 1981 | F | 5 | 4 | 4 | 4 | 4 | 4 | 4 | 3 | 4 | 4 | 2 |
| | | M | 3 | 3 | 3 | 3 | 3 | 2 | 2 | 2 | 2 | 2 | 2 |
| KUR | 1982 | F | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | |
| | | M | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| KUR | 1983 | F | 0 | | | | | | | | | | |
| | | M | 4 | 3 | 3 | 3 | 3 | 3 | 2 | 3 | 3 | | |
| KUR | 1984 | F | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | | | |
| | | M | 4 | 3 | 2 | 2 | 2 | 2 | 2 | 2 | | | |
| KUR | 1985 | F | 3 | 3 | 3 | 3 | 3 | 3 | 3 | | | | |
| | | M | 2 | 2 | 2 | 2 | 2 | 2 | 2 | | | | |
| KUR | 1986 | F | 0 | | | | | | | | | | |
| | | M | 1 | 1 | 1 | 1 | 1 | 1 | | | | | |
| KUR | 1987 | F | 3 | 3 | 3 | 3 | 3 | | | | | | |
| | | M | 1 | 1 | 1 | 1 | 1 | | | | | | |
| KUR | 1988 | F | 5 | 3 | 3 | 3 | | | | | | | |
| | | M | 2 | 2 | 2 | 2 | | | | | | | |
| KUR | 1989 | F | 4 | 2 | 1 | | | | | | | | |
| | | M | 5 | 5 | 4 | | | | | | | | |
| PHR | 1983 | F | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1[a] | 1 | | |
| | | M | 8 | 5 | 6 | 6 | 5 | 6 | 6 | 2[a] | 5 | | |

*Table 1.* Continued.

| Island | Year | Sex | No. tagged | Number seen in year X | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| PHR | 1984 | F | 8 | 8 | 6 | 4 | 4 | 4 | 4[a] | 4 | | | |
| | | M | 5 | 4 | 4 | 3 | 4 | 3 | 1[a] | 4 | | | |
| PHR | 1985 | F | 6 | 5 | 4 | 4 | 4 | 2[a] | 5 | | | | |
| | | M | 9 | 7 | 8 | 7 | 5 | 3[a] | 7 | | | | |
| PHR | 1986 | F | 7 | 7 | 7 | 5 | 6[a] | 7 | | | | | |
| | | M | 10 | 7 | 6 | 6 | 1[a] | 4 | | | | | |
| | | U | 1 | 0 | 0 | 0 | 0 | 0 | | | | | |
| PHR | 1987 | F | 7 | 6 | 5 | 1[a] | 4 | | | | | | |
| | | M | 14 | 10 | 10 | 3[a] | 9 | | | | | | |
| PHR | 1988 | F | 5 | 4 | 3[a] | 5 | | | | | | | |
| | | M | 12 | 11 | 2[a] | 9 | | | | | | | |
| PHR | 1989 | F | 6 | 2[a] | 5 | | | | | | | | |
| | | M | 8 | 0[a] | 6 | | | | | | | | |
| LIS | 1982 | F | 6 | 6 | 5 | 6 | 6 | 4 | 1[a] | — | 2 | 2 | |
| | | M | 7 | 5 | 5 | 5 | 5 | 5 | 3[a] | — | 4 | 1 | |
| LIS | 1983 | F | 18 | 14 | 14 | 14 | 14 | 5[a] | — | 9 | 9 | | |
| | | M | 6 | 6 | 6 | 5 | 5 | 3[a] | — | 4 | 3 | | |
| LIS | 1984 | F | 5 | 5 | 3 | 2 | 1[a] | — | 3 | 2 | | | |
| | | M | 10 | 9 | 9 | 9 | 6[a] | — | 6 | 5 | | | |
| LIS | 1985 | F | 9 | 9 | 8 | 3[a] | — | 3 | 3 | | | | |
| | | M | 5 | 5 | 4 | 3[a] | — | 2 | 2 | | | | |
| LIS | 1986 | F | 9 | 8 | 4[a] | — | 4 | 4 | | | | | |

*Table 1.* Continued.

| Island | Year | Sex | No. tagged | Number seen in year X | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| | | M | 11 | 10 | 8[a] | — | 9 | 8 | | | | | |
| LIS | 1987 | F | 6 | 4[a] | — | 4 | 2 | | | | | | |
| | | M | 12 | 3[a] | — | 4 | 4 | | | | | | |
| LIS | 1988 | F | 8 | — | 7 | 6 | | | | | | | |
| | | M | 10 | — | 8 | 7 | | | | | | | |
| LIS | 1989 | F | 0 | | | | | | | | | | |
| | | M | 0 | | | | | | | | | | |
| LAY | 1983 | F | 10 | 10 | 10 | 9 | 8 | 9 | 9 | 6 | 6 | | |
| | | M | 10 | 9 | 10 | 4 | 3 | 3 | 3 | 2 | 2 | | |
| LAY | 1984 | F | 13 | 12 | 10 | 10 | 8 | 7 | 6 | 6 | | | |
| | | M | 16 | 15 | 15 | 13 | 13 | 11 | 10 | 9 | | | |
| LAY | 1985 | F | 14 | 10 | 9 | 9 | 7 | 5 | 5 | | | | |
| | | M | 16 | 13 | 11 | 10 | 7 | 6 | 5 | | | | |
| LAY | 1986 | F | 17 | 12 | 12 | 9 | 7 | 6 | | | | | |
| | | M | 15 | 13 | 13 | 11 | 9 | 7 | | | | | |
| LAY | 1987 | F | 15 | 13 | 11 | 9 | 7 | | | | | | |
| | | M | 13 | 11 | 5 | 4 | 4 | | | | | | |
| LAY | 1988 | F | 17 | 11 | 5 | 4 | | | | | | | |
| | | M | 23 | 13 | 6 | 7 | | | | | | | |
| LAY | 1989 | F | 13 | 6 | 6 | | | | | | | | |
| | | M | 16 | 9 | 8 | | | | | | | | |
| FFS | 1984 | F | 39 (43)[b] | 35 | 35 | 33 | 30 | 28 | 26 | 26 | | | |

*Table 1.* Continued.

| Island | Year | Sex | No. tagged | Number seen in year *X* | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| | | M | 46 (49)$^b$ | 40 | 38 | 31 | 30 | 29 | 21 | 21 | | | |
| FFS | 1985 | F | 36 (38)$^b$ | 35 | 33 | 29 | 29 | 22 | 20 | | | | |
| | | M | 47 | 45 | 37 | 35 | 32 | 24 | 21 | | | | |
| FFS | 1986 | F | 43 (48)$^b$ | 43 | 38 | 35 | 28 | 22 | | | | | |
| | | M | 51 (52)$^b$ | 44 | 38 | 33 | 24 | 21 | | | | | |
| FFS | 1987 | F | 51 | 46 | 42 | 29 | 24 | | | | | | |
| | | M | 55 | 50 | 45 | 32 | 28 | | | | | | |
| FFS | 1988 | F | 54 (62)$^b$ | 39 | 22 | 21 | | | | | | | |
| | | M | 52 | 38 | 31 | 21 | | | | | | | |
| FFS | 1989 | F | 47 (50)$^b$ | 36 | 23 | | | | | | | | |
| | | M | 51 | 32 | 23 | | | | | | | | |

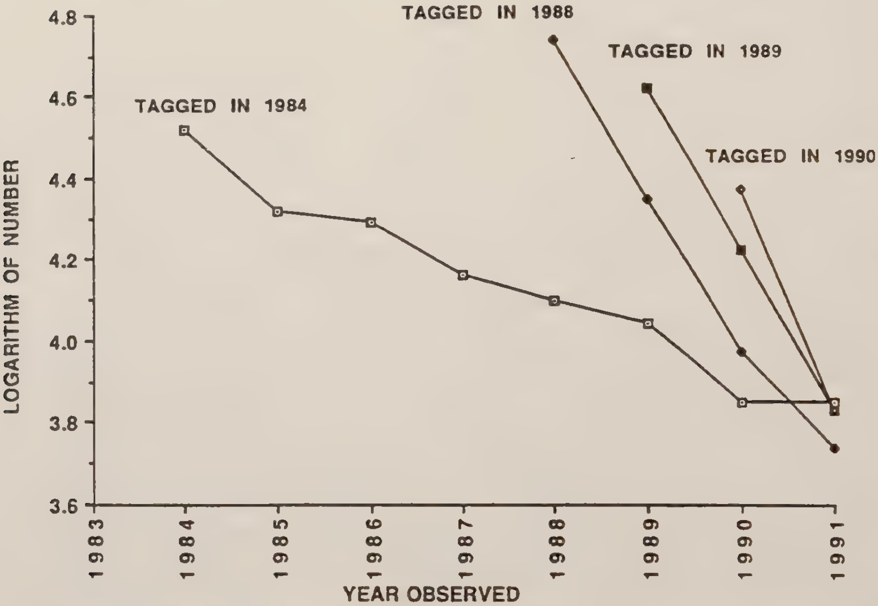

*Figure 2.* Logarithms of resightings of tagged seals at French Frigate Shoals. First points in each series are number tagged.

Most of the births occurred on the two northernmost islands (Westlake and Gilmartin 1990). Only a short duration field camp was possible in 1990, so that the number of resightings dropped sharply in that year. However, the number of sightings rose again in 1991, indicating that survival remained high (Table 1). When another year or two of data have been collected, adjustments of the type utilized in Equation 6 may serve to permit utilization of the 1990 data. However, for the present, we have used regression calculations (Equation 2) for cohorts tagged in 1983 through 1987 to estimate survival beyond the first year. First-year survival was estimated as the ratio of the total seals known to be alive one year after tagging to the total tagged for the years 1983 through 1987, or 62/77 = 0.80 (this calculation involves "back-correcting" two individuals not observed in the first year after tagging but seen in later years). Survival from the regression calculations was: 1983, 0.98; 1984, 0.93; 1985, 0.99; 1986, 0.94 and 1987, 0.93. For pooled survival data through 1989, Equation 4 gave a survival rate of 0.94 (95% B.C.L.: 0.88 to 0.98).

*Lisianski Island*—Only a short field camp was established on Lisianski Island in 1988 and resightings in that year dropped rather sharply. Also, no field camp was present at Lisianski Island in 1989. However, of the 18 weaned pups tagged in 1988, 15 were seen in 1991, and 13 in 1992. Survival calculations by the regression method for cohorts of weaned pups tagged in 1983 through 1986 gave: 1983, 0.92; 1984, 0.90; 1985, 0.77 and 1986, 0.90. First-year survival using back-corrected data for 1982 through 1987 was 88/104 = 0.85.

*Laysan Island*—Annual field camps of long duration that have included pup

*Table 2.* Survival estimate by the Chapman-Robson estimator for monk seals tagged at weaning on French Frigate Shoals. First-year survival not included.

| Year tagged | Survival | | |
|---|---|---|---|
| | Female | Male | Combined |
| 1984 | 0.94 | 0.91 | 0.93 |
| 1985 | 0.93 | 0.89 | 0.91 |
| 1986 | 0.90 | 0.86 | 0.88 |
| 1987 | 0.91 | 0.90 | 0.91 |

tagging have been maintained on Laysan Island since 1983. First-year survival using back-corrected data for 1983 through 1987 gave 119/139 = 0.86 (only one individual was not seen in the first year, but subsequently observed). Inasmuch as field camps were present on Laysan Island in all recent years, an overall estimate by Equation 4 was calculated as 0.85 (95% B.C.L.: 0.81 to 0.88) from the cohorts tagged from 1983 through 1989. Separate estimates for males and females gave 0.82 (95% B.C.L.: 0.73 to 0.86) and 0.87 (95% B.C.L.: 0.81 to 0.91), respectively. Using resightings through 1988 of the first 4 cohorts tagged (1983 through 1986) gives an estimate of 0.89 (95% B.C.L.: 0.84 to 0.94) for males and females combined.

*French Frigate Shoals*—This large atoll is geographically similar to Pearl and Hermes Reef in that the seals use a substantial number of islands, some of small size and difficult to access, making a difficult task of detecting seal tag numbers. However, resighting effort here is much greater due to annual field camp presence of 4–6 mo.

Back-corrected first-year survival from 1984 through 1987 was 344/383 = 0.90, somewhat higher than on any of the the other sites. However, first-year survival has appeared to drop sharply in recent years, along with the appearance of sizable numbers of pups and immature seals in poor physical condition. Survival of tagged seals over all tagged cohorts also appears to have declined since 1988 or 1989. This sharp decline in recent survival is very evident in comparison with the numbers sighted from seals tagged in 1984 (Fig. 2).

The larger samples at French Frigate Shoals (Table 1) make it feasible to consider separate survival estimates for males and females. Female survival was somewhat higher than that of males based on use of Equation 2 to calculate the estimates given in Table 2. Only resightings through 1989 were used in this calculation, due to the evidence of a drop-off in survival beginning in 1989 (Fig. 2). Pooling data through 1989 from cohorts tagged from 1984 through 1987 gave a survival estimate using Equation 4 for females of 0.93 (95% B.C.L.: 0.90 to 0.96) and 0.90 (95% B.C.L.: 0.86 to 0.93) for males. The estimates given thus far used all or part of the successive resightings to estimate survival for a cohort of seals tagged in a given year. This pooling was necessary due to the small samples available. With the larger samples from French Frigate Shoals, it was possible to examine estimates for individual years. For females tagged from 1984 through 1986, the results suggest a higher survival rate for seals born in the first years of the study (Table 3).

*Table 3.* Annual survival estimates for female monk seals tagged at weaning on French Frigate Shoals using the Jolly-Seber estimator.

| Year tagged | Year of estimate | | | |
|---|---|---|---|---|
| | 1984–1985 | 1985–1986 | 1986–1987 | 1987–1988 |
| 1984 | 0.90 | 1.00 | 0.95 | 0.88 |
| 1985 | | 0.97 | 0.94 | 0.98 |
| 1986 | | | 1.00 | 0.94 |

## Discussion

In assessing the results given here, it is important to note that nearly all of the seals in a cohort of weaned pups were tagged in most years, so that the overall survival of a given cohort is recorded by subsequent resighting data (apart from those relatively few cases where a tagged seal was not seen in one year, but was seen subsequently). In many reports of survival calculations, data on a sample of a much larger population are reported. Standard errors may then largely reflect variability introduced by using samples to estimate survival rates. In the present example similar variability results, but the fluctuations are due almost exclusively to chance processes governing whether individual seals lived or died, because all or nearly all seals in a given year-class were tagged.

Discussions of the observed variability are thus not so much concerned with "reliability" of the data as they are with what might have happened to the population by chance; *i.e.*, to some hypothetical population of seals living under identical circumstances to the cohorts actually observed. Because the major purpose of the overall study is to assess the threats to monk seal survival and seek methods for restoration of this endangered population, we need to base decisions on the observed results, and thus have not given much emphasis to variance estimates here.

The monk seal population at Kure Atoll declined severely during the 1960–1970s due to human occupation of Green Island and associated disturbance of pupping beaches (Kenyon 1972). In 1981 a program was initiated to rebuild that population (Gerrodette and Gilmartin 1990), and it appears to have been successful (VanToorenburg *et al.* 1993). With a reduction in human disturbance, the primary birth site has returned to its original location on Green Island (Gerrodette and Gilmartin 1990, Westlake and Gilmartin 1990). The very high survival rates at Kure Atoll suggest that a monk seal population with ample resources can do very well indeed. As is most evident at Kure Atoll, but also apparent at the other sites, and is common in most species of large mammals, first-year survival is lower than that observed in subsequent years.

Survival at Pearl and Hermes Reef, while not as high as at Kure Atoll, is nonetheless adequate to allow population growth, as confirmed by the fact that an initial small population has been increasing steadily over the years of the study (NMFS, unpublished data). Overall survival rates at Laysan and Lisianski Islands seem likely to be generally similar, and appreciably lower than at the other sites. Populations at both islands are not increasing and may be decreasing, a result that we believe is associated with the "mobbing" phenomenon, in which an excess of adult males has caused numerous injuries and outright deaths of adult females in breeding attempts (Hiruki *et al.* 1993). The high survival (0.95) for the first few years at Lisianski Island may well be a consequence of the fact that the younger seals are less affected by the "mobbing" phenomenon, which is mainly noted as individuals approach the breeding age of 5–7 years (NMFS, unpublished data). With the prospect that survival may be lower as individuals, especially females, approach the breeding age, the simple model used here becomes of uncertain utility. Unfortunately, the small sample sizes available make it unlikely that more complex models or statistical tests may be of much help in analysis of the survival data alone. Combining survival, reproductive, and trend count data will be required to clarify the situation at Laysan and Lisianski Islands.

The main pupping site at French Frigate Shoals is East Island (Westlake and Gilmartin 1990) which was the site of military occupation from 1944 to 1952. After abandonment of the site by the U.S. Coast Guard in 1952, pup production at French Frigate Shoals increased substantially (Gerrodette and Gilmartin 1990) and the monk seal population built up rapidly, leveling off in the mid-1980s (NMFS, unpublished data). This population differs in this respect from all of the other sites in that it was small in the late 1950s, when all of the other populations were large, then it increased very substantially, reaching an asymptote in the late 1980s. First-year survival of 0.90 from 1984 through 1987 was a little higher than any other site. The recent dramatic change in immature survival at French Frigate Shoals (apparent in the resighting data since 1989) and other population data suggest this continuing decline is the result of environmental factors affecting food availability, but interpretation is complicated by possible losses of seals in a longline fishery for swordfish in 1990.

Research on the monk seal populations is being continued and intensified. As better understanding of the data and the dynamics of the populations evolves, we believe that more detailed models can be developed for specific analytical purposes.

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**Abstract.**–Field and laboratory procedures were used to acquire dolphin school size estimates from vertical aerial photographs. Multiple photographs were taken of 48 separate schools during a 1989 eastern tropical Pacific (ETP) dolphin abundance survey. During a 12-week "counting period," three readers did independent counts of dolphins in the photographs. For each school, the best photograph imagery was selected and the mean of the three independent counts was used to estimate its "true" size. The coefficient of variation (CV) for school size estimates (between-reader precision) averaged 5.4% and ranged between 1.2% and 14.6%. Most (92%) of the schools were estimated with precision, resulting in a CV of less than 9.0%. Within-reader CV averaged 3.5% and ranged 1.4%–7.1%, indicating that readers were quite precise. To test if reader methods were constant during the counting period, temporal trends in estimates were tested by linear regression analyses and a repeated-counts experiment with repeated measures analysis of variance (RM-ANOVA). Regression analyses indicated no significant temporal trends or bias in the deviation of counts from the means. The RM-ANOVA showed a significant "reader with time" interaction which was attributed to the relatively high variability between readers in counts made at the start of the experiment. Results suggested that methods were constant and counts were precise after an initial "warm-up" counting session.

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# Method and precision in estimation of dolphin school size with vertical aerial photography

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Visual estimation of the number of dolphins in a school is difficult because dolphins dive and the entire school is rarely visible at the sea surface at one time. Shipboard observer estimates can be highly variable and they may be biased (Scott et al., 1985; Anganuzzi and Buckland, 1989). Consequently, estimates of dolphin population abundance derived from visual survey data may be biased, and resulting management decisions aimed at conserving these populations may be inappropriate.

The Southwest Fisheries Science Center (SWFSC) has been conducting surveys to monitor temporal trends in the abundance of eastern tropical Pacific (ETP) populations of the pantropical spotted dolphin (*Stenella attenuata*), spinner dolphin (*S. longirostris*), striped dolphin (*S. coeruleoalba*) and common dolphin (*Delphinus delphis*). These surveys are one part of a multifaceted effort to conserve ETP dolphins subjected to incidental mortality in the international purse-seine fishery for yellowfin tuna, *Thunnus albacares* (Perrin, 1975; Wade and Gerrodette, 1992). Starting in 1987, in response to the problem of potential bias in visual school-size estimates, annual ETP surveys were complemented with aerial photography of dolphin schools. This allowed shipboard-observer estimates to be compared with estimates (of the same schools) taken from counts of dolphins in the photographs.

School size estimates derived from large-format (126-mm) aerial photographs were validated during a 1979 study when five separate schools (size range: 161–396 dolphins) were photographed and then captured in a tuna purse-seine net (Scott et al., 1985). Results showed that dolphin counts from the photographs were not statistically different from counts tallied by hand as dolphins were being released from the net. This suggested that counts from aerial photographs approximated "true" school size.

This report details photographic and counting methods used to derive dolphin[1] school size estimates from large-format vertical aerial photographs. Many of the techniques originated with Scott et al. (1985). The techniques were modified to support the photography and laboratory efforts associated with large-scale ETP dolphin population surveys (i.e., annual surveys of 120 days; covering a 19-million-km$^2$ study area). After a survey in 1989, three readers did independent dolphin counts from approximately 200 dolphin school photographs (multiple photographs were taken for 48 separate schools) over 12 consecutive weeks. For each school, the best photograph imagery was selected (according to criteria described below) and the mean of the three independent counts was used to estimate its true size. The coefficient of variation (CV) was used to characterize the precision (between-

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[1] For purposes of this paper, "dolphin" refers to dolphins as well as small toothed-whales that are included in the photograph sample.

and within-reader) associated with the school size estimates.

One concern was that during the 12-week "counting period," readers might be inconsistent in the application of criteria (cognitive or physical methods, or both) used for counting. If readers were inconsistent, then this might affect the accuracy and precision of the estimates. A two-step approach was taken to address this concern. First, temporal trends in the deviation of counts from the means (see Sokal and Rohlf, 1981, p. 50) were evaluated by linear regression. This approach assumed that the mean of three reader counts was close to the true school size and that the sample error was normally distributed. If individual reader counts were not normally distributed, then this might indicate reader bias or a change in criteria. Second, readers did repeated-counts (at four time points during the counting period) of a known sample of photographed schools. This was done to evaluate the consistency of individual readers (within-reader precision) and to test the hypothesis that dolphin counts (from the same photographs) done at the beginning, middle, and end of the counting period were independent of temporal effects. If the hypothesis proved true, then this would support the idea that counting criteria were constant throughout the counting period.

## Materials and methods

### At sea

Aerial photographs analyzed in this report were taken with Chicago Aerial Industries KA-62 aerial cameras mounted vertically on a Hughes 500-D helicopter. The helicopter was stationed aboard the National Oceanic and Atmospheric Administration (NOAA) survey ship *David Starr Jordan*. All cameras had forward-motion compensation (to minimize photo image blur from aircraft movement) and a 76.2-mm lens. Large-format (126-mm) Kodak Aerochrome MS 2448 color film was used. In order to minimize the behavioral response (scattering and deep diving) of the dolphin schools to the helicopter, photographs were taken at 244 m (800 ft) altitude. The scale of the photographs at this altitude was 1:3200, the sea surface area in a photograph frame was 366 $m^2$, and a 2-m dolphin measured 0.63 mm on the film. The camera cycle rate was programmed to expose for approximately 80% film image overlap, i.e., 80% of the area photographed in one frame was photographed again in the next successive frame. Successive exposed photograph frames for a school were recorded as a complete "photo-pass." To enhance the probability of photographing an entire school, multiple photo-passes (avg.=5) were made over a school.

### In the laboratory

**Counts** Light tables equipped with dissection microscopes (0.7× to 7× variable objective and 10× widefield oculars) were used to view and count the dolphin images during counting. Dolphins were counted by hand-tally while being plotted with a permanent marker on a clear acetate overlay. The marked overlay, when moved to the image overlap area of adjacent frames and aligned over dolphins that were previously plotted, made it easier to identify those dolphins not yet counted in the photo-pass. The photo-pass was the unit on which school size estimates were based (Scott et al, 1985); each pass was counted independently by three readers.

**Criteria for selecting the "true" school size** For each of the 48 photographed schools, the readers chose (by group consensus) the one photo-pass where the mean of the reader counts was the best estimate of true school size. This decision was based on the precision of the three replicate counts and the reader assigned "quality ratings" for the photo-pass. Ratings reflected how confident the reader was in the accuracy of the count. For each photo-pass, readers independently assigned quality ratings ranging from 1 to 4. A rating of "1" indicated that a photo-pass had "excellent" quality. A rating of "2" indicated that the count was "good" despite the presence of some questionable images (i.e., it was difficult to discern and count dolphins accurately when images were partially obscured by light-glare or when photographic resolution was reduced for deep swimming dolphins because of loss of light with sea depth). A photo-pass was rated "3" or "fair" when more questionable images were encountered, but readers still believed the count was a close approximation of true school size. A photo-pass rated "4" was deemed unusable for size estimation because the reader felt there were too many questionable images and the count was not a reliable estimate of true school size.

One source of between-reader variation in dolphin photograph counts was reader error, where dolphins were missed or counted twice. Variation also occurred because readers differed in their interpretations of whether questionable images were dolphins or merely background water turbulence in the photographs. Based on the premise that "precision leads to accuracy" (Sokal and Rohlf, 1981), for each photo-pass, the CV of the three independent counts was used to monitor the reliability of the school size estimate. For photo-passes where the CV of the counts exceeded 10%, the dolphin school was re-counted (independently) to see if the precision of the estimate could be improved. If the CV was above 15% after a second count, the photo-pass was excluded from the study because the counts were considered too variable and little confidence was placed in the accuracy of the estimate.

**Analytical methods** The CV was plotted against the variables "school size" and "quality rating" to evaluate how different school sizes and photograph image qualities affected precision. The CV was also used to characterize the precision of individual readers in repeated-counts as described below.

The percent deviation (PD) is a measure of how distant (+ or −) a count is from the mean. Because this difference is expressed as a percentage of the mean, the PD is a consistent index of deviation relative to changes in the mean. For the PD, let $x_{ij}$ be the $i$th reader's determination of the size of school $j$. The average determination (or mean) over three readers of the size of the $j$th school was given by

$$\bar{x}_{.j} = \frac{1}{3}\sum_{i=1}^{3} x_{ij} \ . \qquad (1)$$

The PD of $x_{ij}$ is expressed as

$$PD_{ij} = \frac{x_{ij} - \bar{x}_{.j}}{\bar{x}_{.j}} * 100 \ . \qquad (2)$$

PD values were plotted to evaluate whether individual reader counts were normally distributed or readers were biased (i.e., tended to count high or low relative to the mean). To test for temporal trends in individual reader counts, PD values were regressed against the variable "time." Time represented the chronological sequence, unique for each reader, in which the 48 schools were counted. Logistically, it was impractical for readers to follow the same sequence in working with the photo-passes.

For the repeated-counts experiment, a known sample of six photographed dolphin schools (henceforth referred to as the "experiment schools"), which varied in school size and image quality, were counted four times. Counts were done once at the start of the counting period, then again every 25 days during the period. Changes with time (temporal trends) due to the variables of "school size," "image quality," and "reader" were tested by using a repeated measures analysis of variance (RM-ANOVA) model from Winer (1971; p. 337).[2] Outlier counts were identified by using Shapiro-Wilk's test for normality at $\alpha = 0.05$ (Shapiro and Wilk, 1965). After log-transformation, data met $F$-test requirements of homoscedasticity according to Levene's test at $\alpha = 0.05$ (computer program BMDP7D used, Dixon et al. 1988). The RM-ANOVA was computed using the software program SuperANOVA (Abacus Concepts, 1990).

## Results and discussion

Scott et al. (1985) reported that dolphin school size estimates derived from aerial photographs were accurate and more precise than visual estimates. They found the standard deviation of estimates (log-transformed) averaged 6% of school size for photographic estimates and 10%–30% of school size for visual estimates. The CV for estimates (untransformed) of the 11 schools used in their precision analysis averaged 8.4% (range: 3.7%–15.1%) indicating slightly less precision when compared with estimates presented here (avg. CV: 5.4%; range: 1.2%–14.6%; Table 1). The difference is explained, in part, by their statistical model, which accounted for variance due not only to independent repetitive counts (2 to 4 per photo-pass), but also due to camera types (126- and 229-mm formats) and multiple photo-passes (2 to 7) for a given school. In the present study, variability was minimized by use of one type of camera (126-mm format) and by including only counts of the single best photo-pass for a school.

School size estimates averaged 146 and ranged between 4 and 633 (Table 1). Most schools (92%) were estimated with precision that resulted in a CV of less than 9.0%, and precision varied little with school size (Fig. 1 and Table 2). Estimate precision tended to decrease with decreased quality of the dolphin school photographs (Fig. 2). PD values (listed in Table 1) plotted for individual readers appeared normally distributed, indicating no between-reader bias in counts of the dolphin images.

Repeated-count data are presented in Table 3. Outlier values for experiment school number III (Table 3) resulted from reader error when dolphins were missed as the marked acetate was moved from the dolphin low density area of the photo-pass (in this case, the beginning of the photo-pass) to the high density area. Alternatively, when dolphins in the high density area were counted first, the precision of the estimate was improved because the majority of dolphins in the school were plotted and counted at the onset; this made it easier to track individual dolphins on adjoining frames.

Within-reader CV for repeated counts averaged 3.5%. Reader 2, the most experienced reader, was most precise in repeated counts (avg. CV: 2.6%; range: 1.4–3.8%) followed by reader 3 (avg. CV: 3.4%, range: 1.5–5.1%), and Reader 1 (avg. CV: 4.7%, range: 2.5–7.1%). The RM-ANOVA showed significant differences between

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[2] Model detailed in: Gilpatrick, J. W. Jr. (1992). Using vertical aerial photographs to estimate dolphin school sizes: precision and consistency. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-92-35, 20 p.

**Table 1**

Counts, mean school size, CV, average quality ratings, and PD values for schools photographed in the 1989 ETP dolphin population survey.

| School no. | Species codes[1] | Reader counts[2] R1 | R2 | R3 | Mean school size | CV (%) | Avg. quality rating[3] | Reader PD[4] R1 | R2 | R3 |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | S.COE | 37 | 35 | 39 | 37.0 | 5.4 | 1.3 | 0.0 | –5.4 | +5.4 |
| 2 | S.ATT | 250 | 227 | 221 | 232.7 | 6.6 | 2.7 | +7.5 | –2.4 | –5.0 |
| 3 | S.LON | 153 | 139 | 147 | 146.3 | 4.8 | 1.0 | +4.6 | –5.0 | +0.5 |
| 4 | S.COE | 57 | 54 | 56 | 55.7 | 2.7 | 2.3 | +2.4 | –2.9 | +0.6 |
| 5 | S.ATT/S.LON | 124 | 127 | 130 | 127.0 | 2.4 | 2.3 | –2.4 | 0.0 | +2.4 |
| 6 | S.ATT/S.LON | 192 | 196 | 216 | 201.3 | 6.4 | 1.7 | –4.6 | –2.7 | +7.3 |
| 7 | S.ATT/S.LON | 274 | 236 | 242 | 250.7 | 8.2 | 1.0 | +9.3 | –5.9 | –3.5 |
| 8 | S.COE | 48 | 47 | 49 | 48.0 | 2.1 | 1.0 | 0.0 | –2.1 | +2.1 |
| 9 | F.ATT | 17 | 18 | 18 | 17.7 | 3.3 | 1.0 | –3.8 | +1.9 | +1.9 |
| 10 | S.ATT/S.LON | 81 | 78 | 77 | 78.7 | 2.7 | 1.0 | +2.9 | –0.9 | –2.1 |
| 11 | S.ATT/S.LON | 412 | 416 | 398 | 408.7 | 2.3 | 1.3 | +0.8 | +1.8 | –2.6 |
| 12 | S.ATT/S.LON | 101 | 106 | 118 | 108.3 | 8.1 | 2.3 | –6.8 | –2.2 | +8.9 |
| 13 | S.LON | 20 | 20 | 21 | 20.3 | 2.8 | 2.7 | –1.6 | –1.7 | +3.3 |
| 14 | S.ATT/S.LON | 107 | 113 | 113 | 111.0 | 3.1 | 1.3 | –3.6 | +1.8 | +1.8 |
| 15 | S.ATT | 118 | 124 | 109 | 117.0 | 6.5 | 1.3 | +0.9 | +5.9 | –6.8 |
| 16 | S.ATT/S.LON | 618 | 607 | 675 | 633.3 | 5.8 | 2.0 | –2.4 | –4.2 | +6.6 |
| 17 | P.ELE | 400 | 391 | 399 | 396.7 | 1.2 | 1.0 | +0.8 | –1.4 | +0.6 |
| 18 | S.COE | 58 | 53 | 60 | 57.0 | 6.3 | 1.3 | +1.8 | –7.0 | +5.3 |
| 19 | S.COE | 52 | 55 | 61 | 56.0 | 8.2 | 1.7 | –7.1 | –1.8 | +8.9 |
| 20 | D.DEL | 317 | 323 | 326 | 322.0 | 1.4 | 1.0 | –1.6 | +0.3 | +1.2 |
| 21 | D.DEL | 326 | 312 | 367 | 335.0 | 8.5 | 1.3 | –2.7 | –6.9 | +9.6 |
| 22 | S.COE | 24 | 23 | 25 | 24.0 | 4.2 | 1.3 | 0.0 | –4.2 | +4.2 |
| 23 | G.MAC | 19 | 18 | 19 | 18.7 | 3.1 | 1.0 | +1.8 | –3.6 | +1.8 |
| 24 | S.COE | 75 | 77 | 68 | 73.3 | 6.4 | 2.0 | +2.3 | +5.0 | –7.3 |
| 25 | S.COE | 34 | 30 | 32 | 32.0 | 6.3 | 1.3 | +6.3 | –6.3 | 0.0 |
| 26 | S.COE | 166 | 171 | 181 | 172.7 | 4.4 | 1.7 | –3.9 | –0.9 | +4.8 |
| 27 | D.DEL | 66 | 64 | 60 | 63.3 | 4.8 | 1.7 | +4.2 | +1.1 | –5.3 |
| 28 | S.ATT/S.LON | 216 | 216 | 233 | 221.7 | 4.4 | 1.3 | –2.6 | –2.6 | +5.1 |
| 29 | S.ATT | 25 | 24 | 23 | 24.0 | 4.2 | 1.0 | +4.2 | 0.0 | –4.2 |
| 30 | G.GRI | 56 | 64 | 55 | 58.3 | 8.5 | 1.3 | –4.0 | +9.7 | –5.7 |
| 31 | S.BRE | 4 | 4 | 5 | 4.3 | 13.3 | 2.0 | –7.7 | –7.7 | +15.4 |
| 32 | S.LON | 576 | 678 | 548 | 600.7 | 11.4 | 2.3 | –4.1 | +12.9 | –8.8 |
| 33 | S.ATT | 38 | 50 | 49 | 45.7 | 14.6 | 2.7 | –16.8 | +9.5 | +7.3 |
| 34 | S.COE | 40 | 39 | 40 | 39.7 | 1.5 | 1.0 | +0.8 | –1.7 | +0.8 |
| 35 | S.ATT | 88 | 90 | 80 | 86.0 | 6.2 | 1.7 | +2.3 | +4.7 | –6.7 |
| 36 | S.LON | 315 | 324 | 350 | 329.7 | 5.5 | 1.3 | –4.5 | –1.7 | +6.2 |
| 37 | S.COE | 26 | 25 | 24 | 25.0 | 4.0 | 2.0 | +4.0 | 0.0 | –4.0 |
| 38 | S.COE | 150 | 147 | 156 | 151.0 | 3.0 | 2.0 | –0.7 | –2.7 | +3.3 |
| 39 | S.BRE | 36 | 34 | 35 | 35.0 | 2.9 | 1.0 | +2.9 | –2.9 | 0.0 |
| 40 | S.ATT/T.TRU | 284 | 293 | 337 | 304.7 | 9.3 | 2.3 | –6.8 | –3.8 | +10.6 |
| 41 | G.GRI | 20 | 19 | 18 | 19.0 | 5.3 | 1.0 | +5.3 | 0.0 | –5.3 |
| 42 | S.COE | 35 | 34 | 35 | 34.7 | 1.7 | 1.0 | +1.0 | –1.9 | +1.0 |
| 43 | S.COE | 73 | 74 | 88 | 78.3 | 10.7 | 2.0 | –6.8 | –5.5 | +12.3 |
| 44 | S.COE | 154 | 154 | 144 | 150.7 | 3.8 | 1.3 | +2.2 | +2.2 | –4.4 |
| 45 | D.DEL | 450 | 526 | 474 | 483.3 | 8.0 | 1.3 | –6.9 | +8.8 | –1.9 |
| 46 | S.COE | 80 | 87 | 92 | 86.3 | 7.0 | 1.7 | –7.3 | +0.8 | +6.6 |
| 47 | S.COE | 23 | 24 | 23 | 23.3 | 2.5 | 1.3 | –1.4 | +2.9 | –1.3 |
| 48 | S.COE | 39 | 39 | 37 | 38.3 | 3.0 | 2.0 | +1.7 | +1.7 | –3.7 |
| Average: |  | 145.5 | 145.9 | 147.4 | 145.5 | 5.4 | 1.6 |  |  |  |

[1] Species codes: S.COE = *Stenella coeruleoalba*; S.ATT = *S. attenuata*; S.LON = *S. longirostris*; F.ATT = *Feresa attenuata*; P.ELE = *Peponocephala electra*; G.MAC = *Globicephala macrorhynchus*; D.DEL = *Delphinus delphis*; G.GRI = *Grampus griseus*; S.BRE = *Steno bredanensis*; T.TRU = *Tursiops truncatus*. Multiple species codes indicate mixed–species schools.

[2] Reader codes: R1 = Reader 1; R2 = Reader 2; R3 = Reader 3.

[3] Obtained by averaging the three independent reader assigned quality ratings.

[4] PD = percent deviation of reader count from the mean.

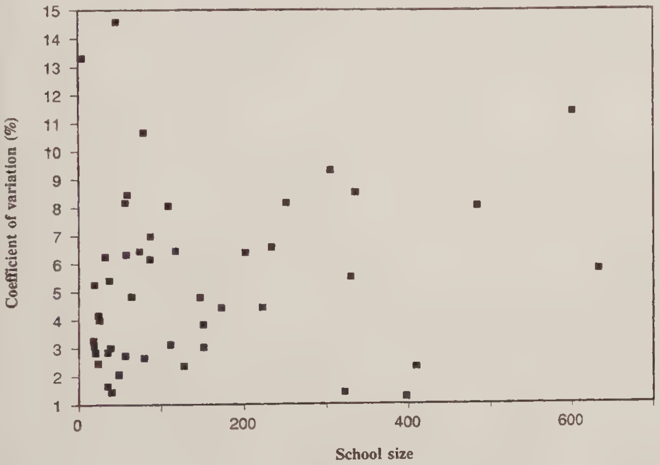

**Figure 1**

Comparison of mean school size and precision (using CV) of count estimates for schools ($n$=48) photographed during the 1989 ETP dolphin population survey.

**Table 2**

Comparison of precision of estimates for small (<125 dolphins), medium (125–350 dolphins), and large (>350 dolphins) schools.

| | CV (%) | |
|---|---|---|
| School size | Mean | Range |
| Small | 5.3 | (1.5–14.6) |
| Medium | 5.2 | (1.4–9.3) |
| Large | 5.7 | (1.2–11.4) |
| overall mean: | 5.4 | |
| overall range: | | (1.2–14.6) |

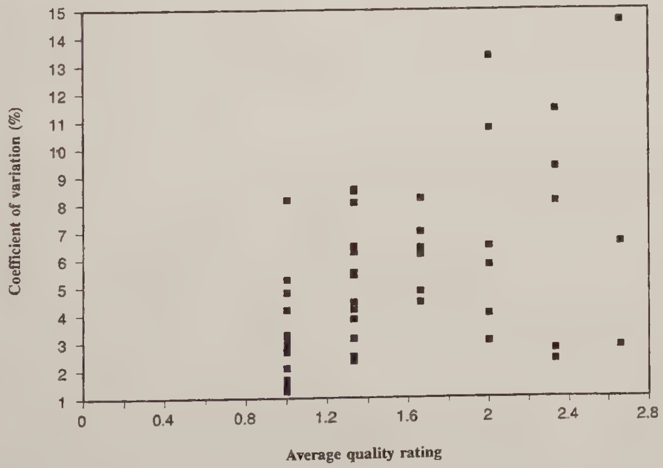

**Figure 2**

Relationship between photograph quality ratings (averaged for three independent readers) and precision (using CV) of count estimates for schools ($n$=48) photographed during the 1989 ETP dolphin population survey.

levels of the factors "school size" and "quality rating" (see between-factors; Table 4). This was expected because photographed schools of different sizes were intentionally selected for the analysis. Often, with RM-ANOVA, between-factor effects are confounded with different levels of the factors (as is true for the two factors above) and it is the temporal trends of the within-factor data that are of primary interest in the analysis (Winer, 1971, p. 299). There were no differences between readers in the overall means of their repeated counts (temporal trends not considered; $P$=0.7898; Table 4).

The $F$ value for the within factor "Time" indicated no significant linear trend for repeated-counts (with the mean of the three reader counts). However, a significant interaction for "reader with time" ($F$=3.503; $P$=0.0258; df=6, 31) indicated there were differences between readers in the respective temporal trends of their repeated-counts (Fig. 3). To investigate the source of the significant effect, the trend data for each reader were tested *a posteriori* by contrasts among means with linear coefficients to weigh the log-transformed data (Sokal and Rohlf, 1981; Abacus Concepts, 1990). Results showed the mean of Reader 1's counts at time one differed significantly from the means of counts made at times two, three, and four ($F$=14.977; $P$=0.0005; df=1). This suggested that Reader 1's counts made at time one were important in causing the significant "reader with time" interaction.

Because the initial counts (at time one) of the experiment schools were done just prior to the start of the 12-week counting period, this suggested that

**Table 3**

Repeated counts experiment. Counts of the experiment schools were done at the start of the 12-week counting period, then repeated every 25 days during the period. Observations in parentheses are outlier values.

| | | | | Time | | | |
|---|---|---|---|---|---|---|---|
| Schools | School size | Quality rating | Reader | Time 1 | Time 2 | Time 3 | Time 4 |
| I | Small | Excellent | 1 | 64 | 64 | 66 | 67 |
| | | | 2 | 69 | 66 | 68 | 70 |
| | | | 3 | 61 | 65 | 64 | 69 |
| II | Small | Good | 1 | 34 | 38 | 38 | 35 |
| | | | 2 | 36 | 35 | 36 | 36 |
| | | | 3 | 38 | 39 | 39 | 38 |
| III | Medium | Excellent | 1 | (191) | 242 | 230 | 236 |
| | | | 2 | 232 | 252 | 236 | 243 |
| | | | 3 | (189) | (193) | (205) | (206) |
| IV | Medium | Good | 1 | (169) | 214 | 194 | 203 |
| | | | 2 | 207 | 211 | 209 | 206 |
| | | | 3 | 213 | 195 | 194 | 205 |
| V | Large | Excellent | 1 | 401 | 468 | 468 | 450 |
| | | | 2 | 457 | 450 | 429 | 432 |
| | | | 3 | 440 | 451 | 429 | 467 |
| VI | Large | Excellent | 1 | 464 | 516 | 525 | 490 |
| | | | 2 | 541 | 527 | 534 | 496 |
| | | | 3 | 507 | 519 | 534 | 527 |

**Table 4**

Results from repeated measures analysis of variance (RM-ANOVA).

| | df | Sum of squares | Mean square | *F*-value | *P*-value | G.-G.[1] *P*-value |
|---|---|---|---|---|---|---|
| School size | 2 | 8.880 | 4.4400000 | 431.485 | 0.0001 | |
| Quality rating | 1 | 0.290 | 0.2900000 | 28.145 | 0.0003 | |
| Reader | 2 | 0.005 | 0.0020000 | 0.241 | 0.7898 | |
| Error (between factors) | 11 | 0.113 | 0.0100000 | | | |
| Time | 3 | 0.002 | 0.0010000 | 2.504 | 0.0775 | 0.0855 |
| Time * school size | 6 | 0.002 | 0.0003323 | 1.653 | 0.1661 | 0.2365 |
| Time * quality rating | 3 | 0.001 | 0.0003299 | 1.641 | 0.2001 | 0.1883 |
| Time * reader | 6 | 0.004 | 0.0010000 | 3.503 | 0.0092 | 0.0258 |
| Error (within factors) | 31 | 0.006 | 0.0002011 | | | |

[1] *P*-value corresponding to degrees of freedom adjustment using the Greenhouse-Geisser (1959) epsilon factor (=0.692) to correct for correlation of repeated measures. See Anderson (1958); Barcikowski and Robey (1984); Dunn and Clark (1987).

between-reader variance may have been atypically high early in the counting period as well. The regression analyses of PD values with time, however, did not provide strong evidence for this because reader counts were close to the mean values and no significant temporal trends were detected (Fig. 4). Probable cause for the significant effect was that readers were "out of practice" at the start, especially Reader 1. Prior to the

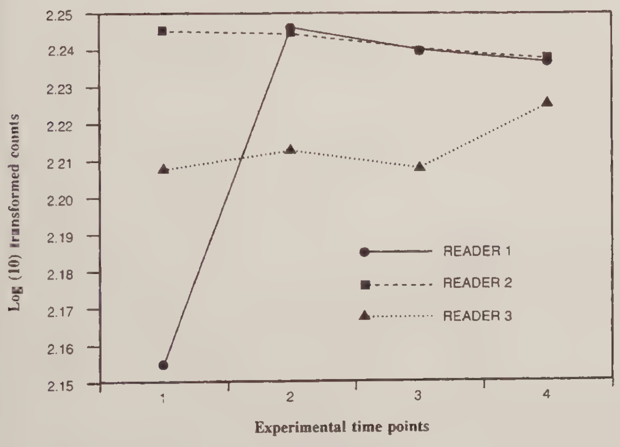

Figure 3

Temporal profiles of the means for counts (log-transformed) made by three independent readers during the repeated-counts experiment.

1991 counting period, a "warm-up" counting session was effective in improving estimate precision, i.e, between-reader CV went from an average of 8% to 4% within one day.

## Conclusion

Results suggest that after a prolonged absence from interpreting dolphin school photographs and doing counts, a warm-up session, where readers are refreshed in counting technique, is important for minimizing reader error and improving precision. Estimate precision is also improved when plotting and counting is initiated at the dolphin high-density area in a photopass. The field and laboratory methods described in this report proved reliable in providing precise dolphin school-size estimates for population abundance studies. The CV statistic and PD index will be used for inter- and intra-annual quality control of dolphin school estimates taken from aerial photographs. The analytical methods used in this paper to describe precision and consistency are applicable to other fisheries and terrestrial wildlife research efforts where independent repetitive counts are conducted for parameter estimation.

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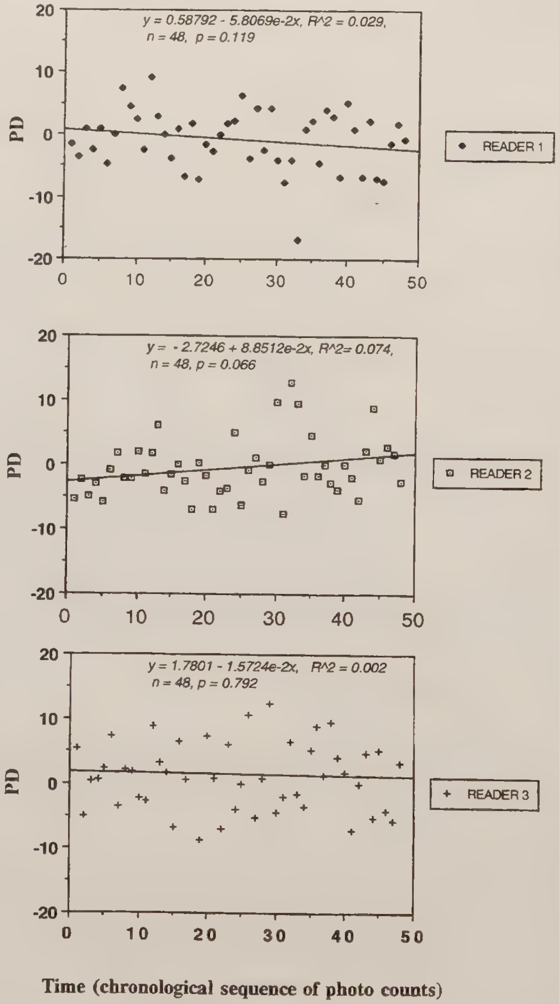

**Figure 4**

Percent deviation (PD) values regressed on "time." Time represented the chronological sequence, unique for each reader, in which photographed schools were counted during the counting period. Zero on the y axis represents the mean count while negative and positive values represent the percent deviation of the count from the mean.

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## Precious Coral Fisheries of Hawaii and the U.S. Pacific Islands

RICHARD W. GRIGG

*ABSTRACT — The precious coral fishery in Hawaii and the Western Pacific consists of one industry but two distinct and separate fisheries. The first is the harvest of black coral by scuba divers from depths of 30–100 m. The second is a fishery for pink and gold coral at depths between 400 and 1500 m and employs either a human-operated submersible that permits selective harvest or tangle net dredges which are nonselective. The modern history of these fisheries date from 1958 until the present. In this paper the ecology, life history, and management of the dominant species that make up these fisheries are reviewed. Research needs of the fisheries and the economic and future prospects of the precious coral industry are also described. At the present, the precious coral jewelry industry in Hawaii (all species) is valued at about $25 million at the retail level.*

### Introduction

Precious corals have been used by humans for the fabrication of coral jewelry since antiquity (Grigg, 1989). Along with amber, precious coral may have also been used as a source of currency for trade by paleolithic man (Tescione, 1968). As a renewable resource in the sea, precious corals are thought to be the slowest growing organisms of any known fishery past or present. Pink and red coral fisheries exist in the Mediterranean Sea and the Pacific Ocean. Black corals are distributed world-wide and small fisheries for black coral exist in all oceans. Hence, precious corals represent a unique and interesting case history of a fishery which is very old and quite widespread and one which renews itself very slowly. In this paper, these aspects of the fishery are considered but only as they relate to the modern history and management of precious coral fisheries in Hawaii and the Western Pacific during the past 35 years. Over this period in this area, two different precious coral fisheries have been developed; one in relatively shallow water between 30–100 m for several species of black coral, and the other, for pink, gold, and bamboo corals at depths of 400–1500 m. A brief history of both fisheries is presented including a description of their ecology and management of target species. Future research needs for both fisheries are described and future prospects of the precious coral industry are considered.

### Taxonomy

Briefly, all species of precious coral in the Western Pacific belong to one of three Orders within the Class Anthozoa, Phylum Coelenterata. The pink and bamboo corals, *Corallium* spp. and *Lepidisis olapa*, are in the Order Gorgonacea. The Hawaiian gold coral, *Gerardia* sp., is in the Order Zoanthidae and the black corals, *Antipathes dichotoma*, *A. grandis*, *A. ulex*, and *Cirrhipathes anguina*, are all in the Order Antipathidae. Gorgonians are octocorals while the Hawaiian gold and black corals are hexocorals.

### History of the Precious Coral Fishery in Hawaii and the Western Pacific

Commercial beds of black coral were discovered in Hawaii in 1958 by Jack Ackerman and Larry Windley (Stewart, 1962a; Grigg, 1965). This discovery was located 4.8 km due west of Lahaina, Maui, at a depth of 30–75 m along a drop-off known as "stone wall" on the Lahaina Roads Reef. What Ackerman and Windley had discovered were populations of two species of exceedingly large black corals, *Antipathes dichotoma* and *Antipathes grandis* (Fig. 1). Subsequent research has shown that 12 additional species exist in Hawaiian waters but most of these occur at depths below 100 m, and none are large enough or are of sufficient quality to be of commerical value for coral jewelry (Grigg and Opresko, 1977).

The discovery of black coral in Hawaii in 1958 led to the establishment of a small cottage industry that produced curios and black coral jewelry in Lahaina, Maui (Stewart, 1962b). In 1960, John Stewart and Jack Ackerman started a company known as Maui Divers. Over the next ten years, Maui Divers grew steadily under the direction of Clifford Slater, and was joined by about a dozen other small companies. By 1969 the industry collectively was producing about $2 million gross retail sales; part of these sales included imports of pink coral jewelry from Taiwan and Japan.

In 1965, Japanese coral fishermen discovered a huge bed of commercial pink coral at about 400-m depth on the Milwaukee Banks in the Emperor Seamount Chain north of Midway Island near the northwesternmost end of the Hawaiian Archipelago. In terms of significance to the United States, only about 10% of the entire area (the so-called Midway Grounds) exist within the U.S. economic zone (EEZ). Nevertheless, as a result of this discovery, interest in precious coral resources dramatically increased in Hawaii. This stimulated new exploration in the high

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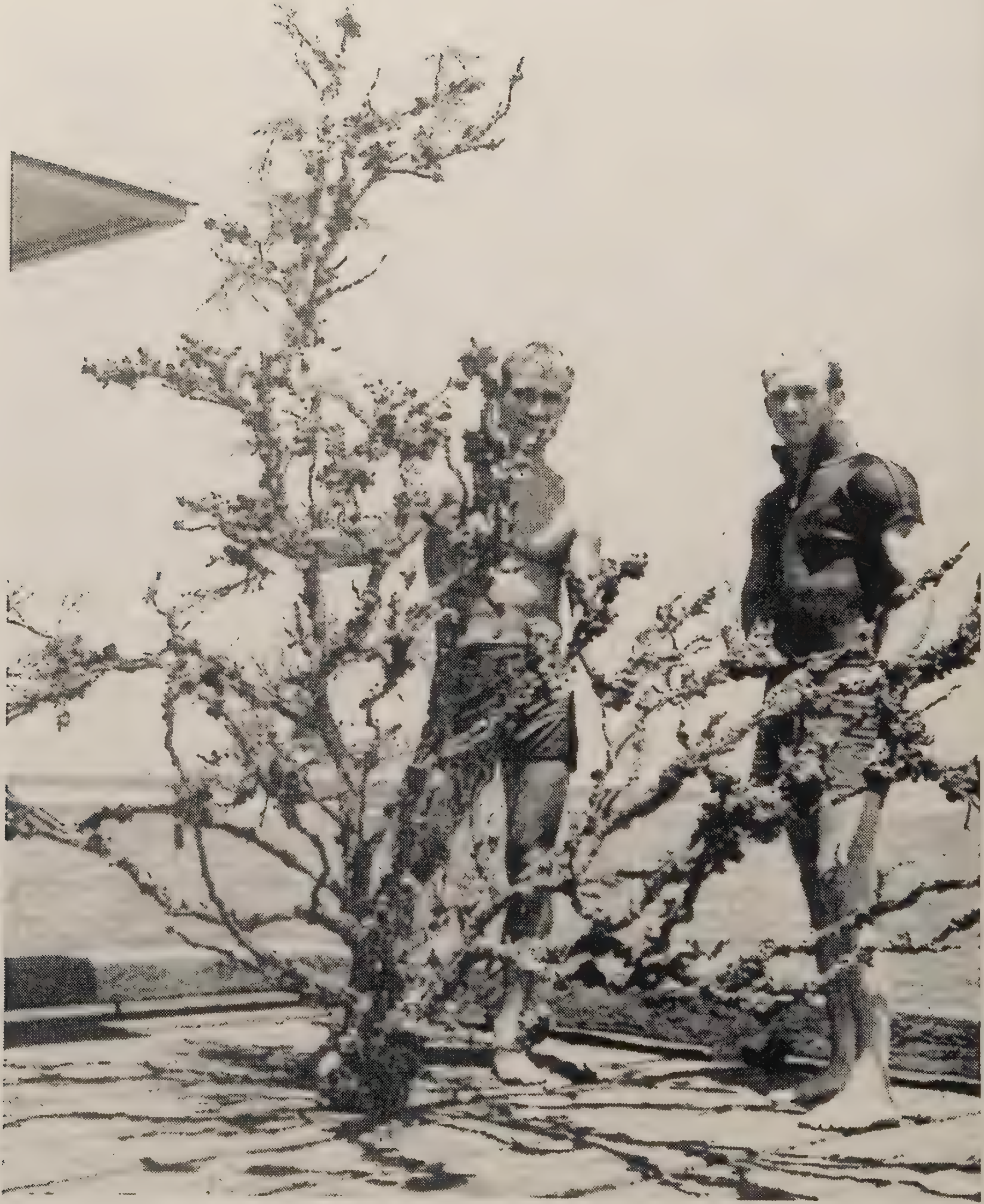

Figure 1.—Jack Ackerman and Larry Windley display a large colony of *Antipathes dichotoma* collected from a depth of 65 m off Lahaina, Maui. The colony is dead and encrusted with numerous sponges and other invertebrates. Even so, the skeleton is still of commercial quality for the manufacture of coral jewelry.

Hawaiian Islands and in 1966, Vernon Brock and Ted Chamberlain of the University of Hawaii discovered a small bed of pink coral *Corallium secundum*, near 400 m depth off Makapuu, Oahu (Fig. 2). In the following three years, a small group of fishermen dredged the Makapuu Bed for pink coral on a small scale using tangle nets (Fig. 3).

In 1970 a long-term research program on precious corals began at the University of Hawaii and this led to the development of a selective harvesting system utilizing a manned submersible (Grigg et al., 1973; Figure 4). In 1973, Maui Divers of Hawaii incorporated this system and began a commerical operation of selective harvest for pink, gold, and bamboo coral which lasted until 1978. The gold coral (*Gerardia* sp.) and bamboo coral (*Lepidisis olapa*) (Muzik, 1978) coexist within the same depth zone and habitat with *Corallium secundum*. The Maui Divers operation lasted 6 years but was discontinued in 1978 because of high operating costs. The annual harvest of pink and gold coral from the Makapuu Bed during this period is given in Table 1. Since this time, the industry in Hawaii has relied on stockpiles of gold coral and exports of pink and red corals (*Corallium* spp.) mostly from Taiwan and Japan. The only other attempt to harvest pink corals domestically within the Western Pacific EEZ was in 1988, when crew members of the vessel *Kilauea* used nonselective tangle nets at Hancock Seamount. Their catch was only 450 kg of *Corallium secundum* and most of the colonies harvested were dead and of low quality.

Because Hawaii's precious coral industry continues to be dependent on sources of raw material outside the US EEZ, it is important to analyze trends in the supply of *Corallium* spp. Pacific-wide. From the time of the major discovery of *Corallium secundum* on the Milwaukee Banks in 1965 to the present, the annual supply of both pink and red corals has been extremely erratic. The harvest of shallow water *Corallium* by Japanese and Taiwanese coral fishermen first peaked in 1969 when production Pacific-wide reached 150 metric tons. Following this boom year, production fell precipitously and remained low for the next five years

**Table 1.—Annual harvest of pink and gold coral from the Makapuu Bed (kg).**

| Year | Gear | *Corallium secundum* | *Gerardia* sp |
|---|---|---|---|
| 1966–69 | Dredge | 1800 | 0 |
| 1970–72 | No harvest | 0 | 0 |
| 1973 | Submersible | 538 | 0 |
| 1974 | Submersible | 2209 | 734 |
| 1975 | Submersible | 1385 | 621 |
| 1976 | Submersible | 400 | 363 |
| 1977 | Submersible | 1421 | 329 |
| 1978 (Jan–June) | Submersible | 474 | 50 |
| 1979–92 | no harvest | 0 | 0 |

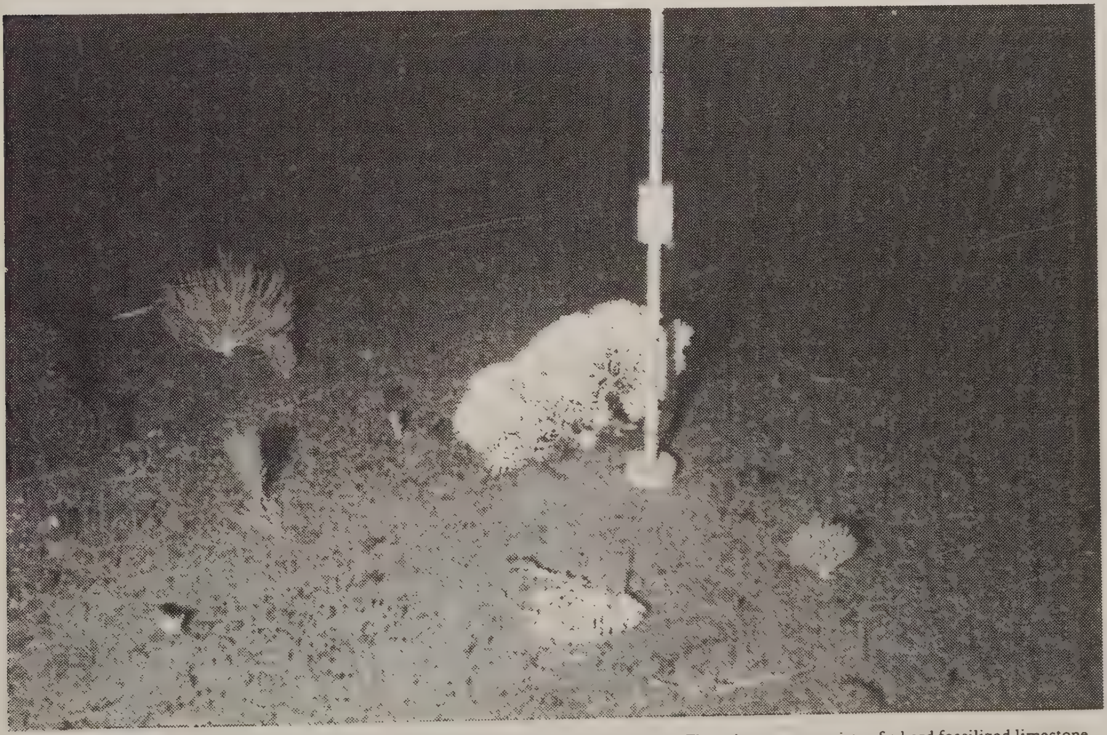

Figure 2.—*Corallium secundum* (center) at a depth of 390 m in the Makapuu coral bed. The substratum consists of a hard fossilized limestone. It is swept by strong bottom currents which prevent the buildup of sediments. The measuring rod is marked at 10 cm intervals.

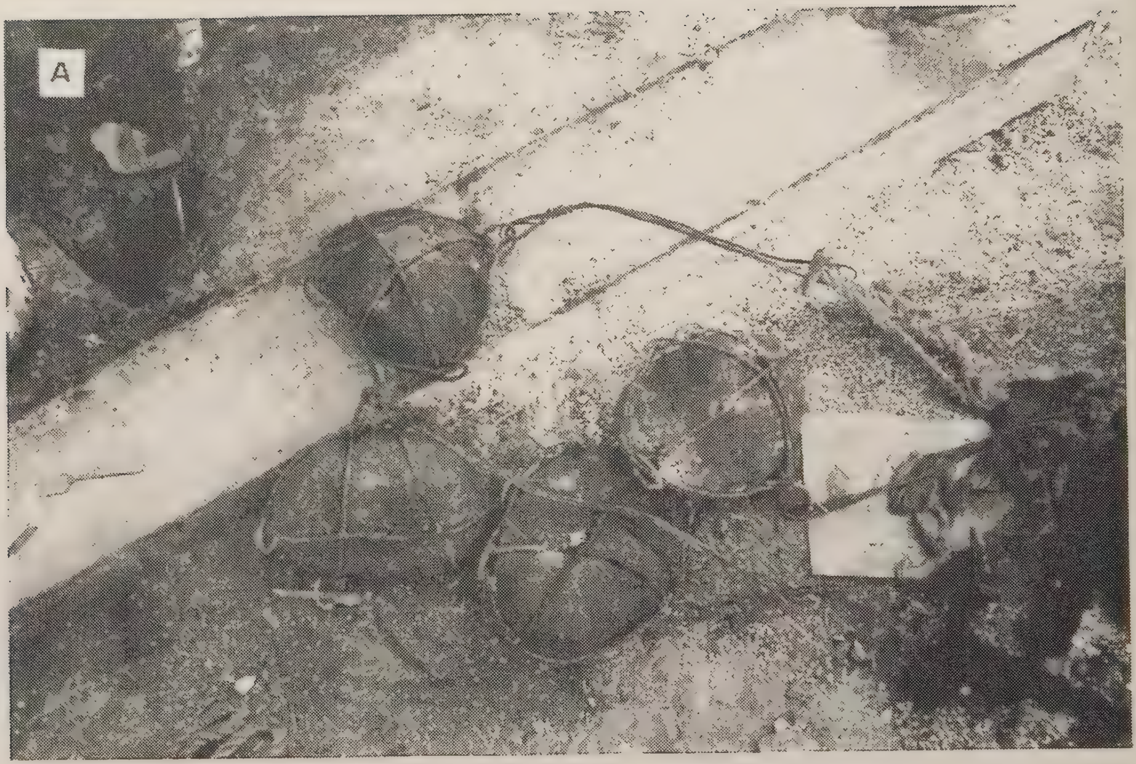

Figure 3.—A = Coral tangle dredges consisting of stones with attached netting.

(Grigg, 1984). Accurate statistics for these years are not available. Then in 1978, a deep-water undescribed species of *Corallium* (sp. nov.) was discovered by a Japanese fishermen at depths between 900 and 1500 m on the Emperor Seamounts. While the color of this species is spotty (sometimes called Scotch), varing between pink and white, it was extremely abundant, and like the 1965 discovery, it produced a "coral rush." In the peak year of 1981, over 100 coral boats from Japan and Taiwan fished the Midway Grounds and production neared almost 300 metric tons (t) Pacific-wide (Table 2). Unfortunately, this intensive fishing effort led to a gradual depletion of the resource, illustrating the well established pattern for all precious coral fisheries: exploration, discovery, exploitation, and depletion (Grigg, 1989).

By 1991, production Pacific-wide stood at an all time low of 2,930 kg (Table 2) and prices of raw material were at unprecedented highs. According to the American Institute in Taiwan, coral production in Taiwan fell to

**Table 2.—Total foreign yield (kg) of precious coral (*Corallium* spp.) in the Pacific during the years 1979–91.**

| Year | Japan<br>Midway grounds | Japan<br>Western Pacific | Japan<br>Submersible | Taiwan (All areas combined) | Total |
|---|---|---|---|---|---|
| 1979 | 76,988 | 14,516 | 0 | 123,000 | 214,504[1] |
| 1980 | 74,228 | 10,227 | 0 | 154,000 | 238,455[1] |
| 1981 | 30,484 | 5,381 | 775 | 254,000 | 290,640[2] |
| 1982 | 52,166 | 3,000 | 551 | 69,200 | 123,917[2] |
| 1983 | 51,087 | 2,947 | 306 | 109,000[3] | 163,493[2] |
| 1984 | 33,164 | 3,315 | 634 | 157,000[3] | 194,113[2] |
| 1985 | 9,322 | 2,366 | 816 | 214,000[3] | 226,504[2] |
| 1986 | 1,650 | 1,268 | 1,261 | 141,000[3] | 146,179[2] |
| 1987 | 585 | 1,986 | 425 | 106,000[3] | 108,977[2] |
| 1988 | 217 | 1,605 | 1,082 | 50,000[5] | 52,094[2] |
| 1989 | 1,961 | 1,057 | 938 | 5,400[6] | 9,156 |
| 1990 | 0 | (2,172[4]) | | 1,000[6] | 3,172 |
| 1991 | 0 | (1,390[4]) | | ~1,000[6] | ~2,930 |

[1] Grigg, 1984.
[2] All Japan Coral Fishing Association.
[3] Coordination Council for North American Affairs, Taipei, Taiwan, D. K. P. Liu.
[4] D. M. Ancona, Embassy of the United States, Tokyo, Japan. Western Pacific and submersible catch combined.
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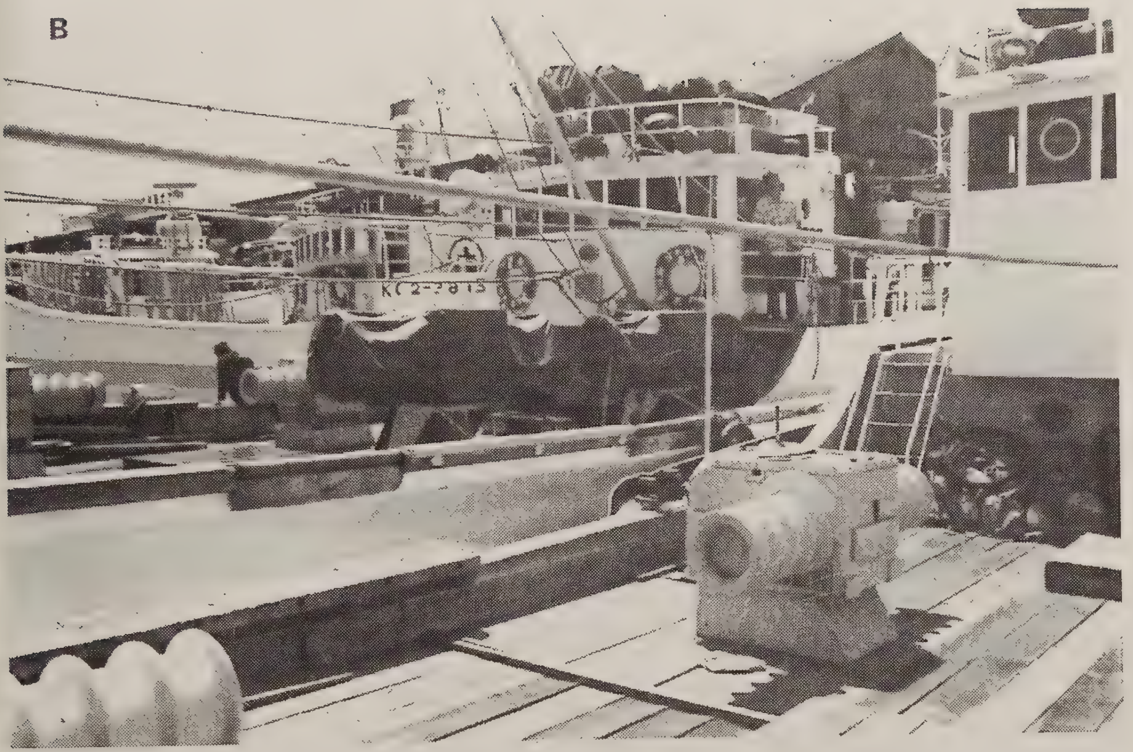

Figure 3.—B = Japanese coral fishing boat showing line haulers, tangle net dredges, and rollers on side of vessel.

1 t in 1990 but exports drawn from previous year stockpiles were 63 t of coral products. As stockpiles of the resource are gradually reduced worldwide, new production will depend on the discovery of new precious coral beds. This boom and bust cycle of harvest and supply dramatically illustrates the need for management of the fishery. Management has been hampered by the multinational character of the fishery and because many precious coral beds exist in international waters.

In contrast to the pink and red coral fishery in the Pacific, the black coral fishery in Hawaii is relatively stable. While demand has fluctuated considerably over the years since its discovery in 1958, the supply of black coral has never failed to meet demand. In the early years of the industry during the 1960's and early 70's, as much as 10,000 kg were harvested annually from the black coral beds off Maui and Kauai. During the late 70's and early 80's the demand for black coral was greatly reduced, being replaced by a higher consumer interest in pink and gold coral. However, since about 1986, demand for black coral has been steadily increasing. Consumption by one company, Maui Divers of Hawaii, Ltd., illustrates this trend (Table 3).

Table 3.—Consumption of Hawaiian black coral by Maui Divers of Hawaii, Ltd., 1982–92.

| Year | Weight (all species combined), kg |
|---|---|
| 1982 | 78 |
| 1983 | 70 |
| 1984 | 257 |
| 1985 | 278 |
| 1986 | 463 |
| 1987 | 934 |
| 1988 | 432 |
| 1989 | 824 |
| 1990 | 1295 |
| 1991 | 1740 |
| 1992 (Jan–July) | 1238 |

Production by Maui Divers of Hawaii accounts for more than 50% of all locally produced black coral jewelry in the State of Hawaii. Today, considerably less black coral is used for fabrication than during the 60's and 70's because the jewelry items produced are smaller and of higher quality and because modern cutting procedures are much more efficient than in the past. In November of 1987, black coral was named the State "Gem" and this has increased consumer interest considerably.

Over the years, the stability of the industry has been aided by the availability of inexpensive black coral from the Philippines and Tonga (Harper, 1988). These sources have filled the demand for low quality but high volume jewelry products. Also black coral resources in Hawaii have been well managed by local fishermen who voluntarily do not harvest colonies below

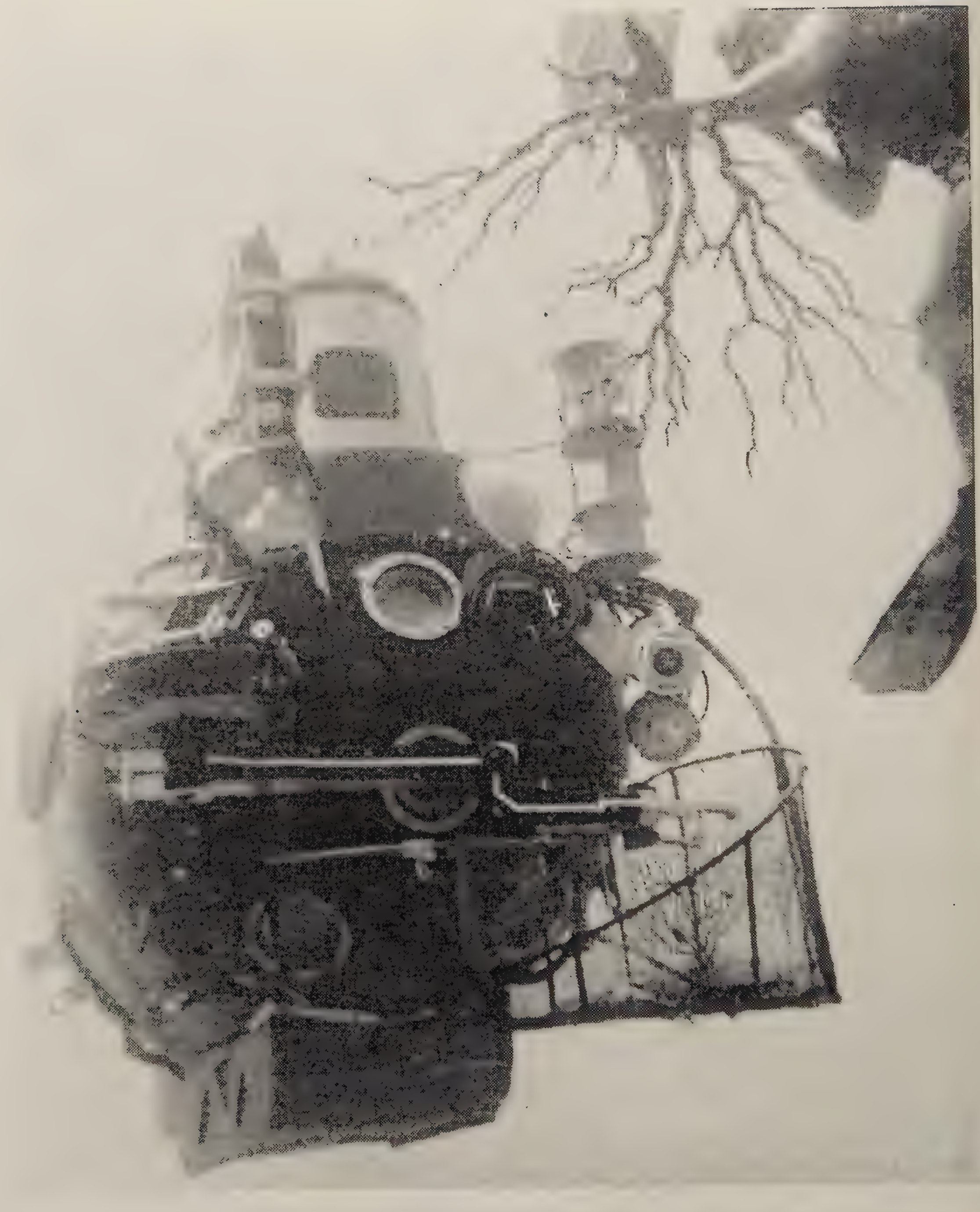

Figure 4.—As the Maui Divers *Star II* submersible approaches the surface, a subtender using scuba collects gold coral, *Gerardia* sp., from the basket.

48 inches (1.2 m) in height. This size limit has been adopted by the Western Pacific Regional Fisheries Management Council and has been recommended to the State of Hawaii and is based on the growth rate and reproductive pattern of *Antipathes dichotoma* and calculations of maximum sustained yield (Grigg, 1976).

Overall, the precious coral industry in Hawaii has steadily grown over the past 34 years since its inception. At the retail level today, the precious coral industry is valued at about $25 million and consists of about 100 retailers.

A small but stable black coral fishery in Hawaii continues to thrive while the fishery Pacific-wide for *Corallium* spp. has drastically declined owing to depletion of the resource. Present demand for *Corallium* is being met largely by the utilization of stockpiles. The future of the *Corallium* fishery will depend on the discovery of new beds of commercial grade species of pink and red coral.

### Ecology of precious corals

The ecology and patterns of life history of various species of precious corals have been reviewed by Grigg (1974, 1976, 1984, 1989). In general, most species of precious corals are slow growing, have low rates of recruitment and mortality, and consequently are relatively long lived. The oldest colonies of *Corallium secundum* in the Makapuu Bed off Oahu probably reach an age of 75 years, and the largest colonies of *Antipathes dichotoma* and *A. grandis* may even be older. Populations of both *Corallium secundum* and both black coral species appear to be recruitment limited (Grigg, 1988). In favorable environments for *Corallium secundum* and *A. dichotoma* in Hawaii, populations are relatively stable suggesting that recruitment and mortality are approximately in steady state. However, in suboptimal environments, the age frequency distributions of both species are very uneven or truncated probably owing to episodic mortality events (personal observation).

Mortality is most often the result of smothering by sediments and by bioerosion of the substrata which leads to toppling of colonies. Fragmentation and reattachment (asexual reproduction) appears to rarely occur. Most species of precious coral are uni-sexual or dioecious, i.e. the sexes are separate. The age of reproductive maturity of *Corallium secundum* and *A. dichotoma* is similar, occurring about age 12–13 which is about one-sixth the longevity of the oldest colonies. Fertilization of Hawaiian precious corals appears to take place externally within the water column. The duration of the larval stage is unknown for most species of precious coral, but studies of one species, *Corallium rubrum*, in the Mediterranean Sea suggest that larvae of this species remain competent for several weeks (Vighi, 1970). In general, settlement is most successful on clean swept surfaces exposed to strong bottom currents. The larvae of both species of *Antipathes* in Hawaii are known to be negatively phototactic which explains why they are not found at shallow depths (< 30 m) and are most abundant beneath overhangs and on other dimly lit surfaces (Grigg, 1965).

The ecological requirements of all species of precious coral in the western Pacific can be briefly summarized as follows. All species require a firm (rocky) substratum free of sediment and most thrive in areas swept by moderate to strong currents. All species lack symbiotic algae in their tissues (ahermatypic) and most are found in deep water below the euphotic zone (Table 4). All species are filter feeders and many are fan-shaped, a growth form which maximizes contact of feeding surfaces with particles or microplankton entrained in the water column. Light and temperature appear to influence larvae more than adults. The lower depth limit of *A. dichotoma* and *A. grandis* coincides with the top of the thermocline in the high Hawaiian islands. Larvae may avoid settling deeper where lower temperature may prevent reproduction (Grigg, 1977, 1984). Species of *Corallium* exist below the euphotic zone at depths between 350 and 1,500 m where temperature varies between 14° and 3°C.

### Resource management

The life history attributes of all species of precious corals in the western Pacific make these living resources highly vulnerable to over-exploitation in unmanaged fisheries. This is because many year classes are exposed to harvesting at the same time. Virtually decades of accumulated standing stock can be collected during short intensive periods of fishing. Indeed, the historical pattern of the fishery worldwide is one of discovery, exploitation and depletion.

Historically, species of *Corallium* have been harvested non-selectively using various types of dredges. In the Meditteranean Sea a heavy wooden cross outfitted with tangle netting (The Cross of Saint Andrew) is dragged across the bottom where corals are broken and entangled in the mesh. Japanese and Taiwanese fishermen also use tangle gear although theirs is simpler in design, consisting of either stones or iron bars with attached netting (Fig. 3). Since the inception of SCUBA, shallow water colonies in the Medit-teranean Sea (up to 110 m in depth) have been harvested selectively by divers. In Hawaii the black coral fishery also employs SCUBA divers who selectively harvest colonies with axes, hammers, and saws (Fig. 4). The first selective harvest of *Corallium* in which a submersible was used by Maui Divers of Hawaii in 1973. This was accomplished with the use of a sophisticated cutter, claw, and basket assembly that was attached to the submersible (Fig. 5, Grigg et al., 1973). Since 1983 an unmanned submersible (robot) has been used in Japan to harvest selective species of precious coral in traditional seas (Table 2).

Precious coral resources in Hawaii and the Western Pacific fall under the

**Table 4.—Depth zonation of all species of precious coral in the western Pacific.**

| Species and common name | Depth range (m) |
|---|---|
| *Corallium secundum*, Angle skin coral | 350–475 |
| *Corallium* sp. nov., Midway deepsea coral | 1000–1500 |
| *Gerardia* sp., Hawaiian gold coral | 300–400 |
| *Lepidisis olapa*, bamboo coral | 350–400 |
| *Antipathes dichotoma*, black coral | 30–100 |
| *Antipathes grandis*, pine black coral | 45–100 |
| *Antipathes ulex*, fern black coral | 40–100 |
| *Antipathes anguina*, wire black coral | 20–60 |

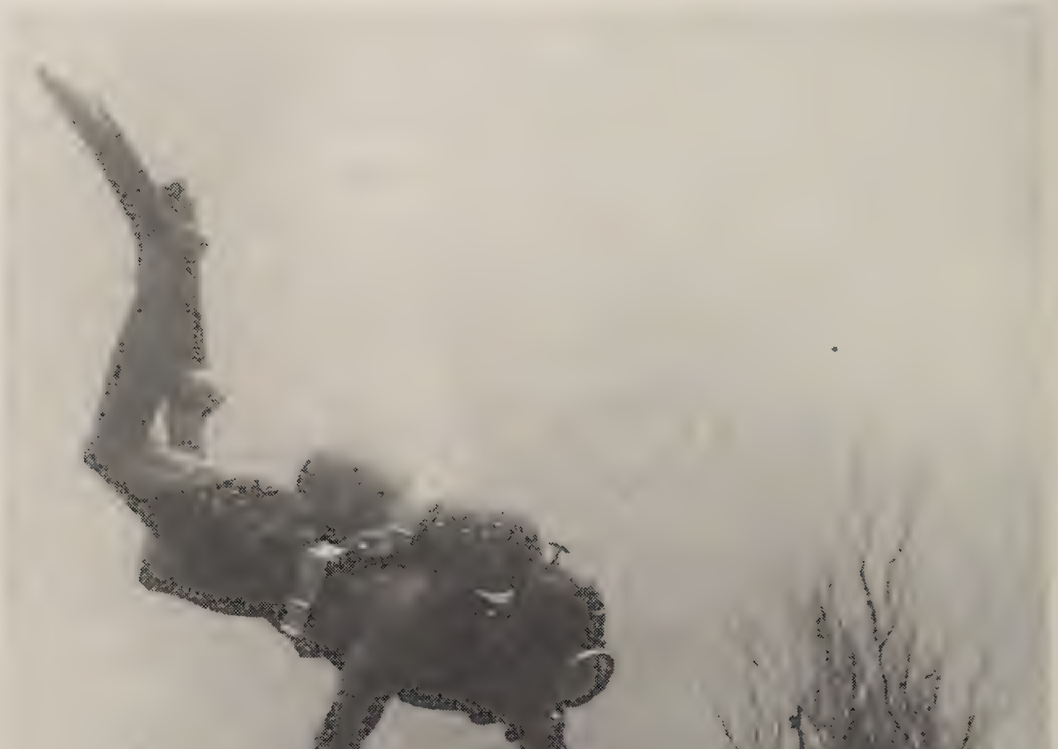

Figure 5.—A black coral diver in Hawaii approaches a small colony of *Antipathes dichotoma* at a depth of 50 m off Lahaina, Maui.

management authority of the State of Hawaii and the U.S. Federal government. The State has clear jurisdiction over resources out to three miles but also claims authority over inter-island waters. Hence the State has declared jurisdiction over the Makapuu Coral Bed situated 9 km (6 miles) off Makapuu in the channel between Oahu and Molokai. Federal jurisdiction extends from 3 miles outside the State of Hawaii, Guam, and American Samoa to 200 miles, and from the shoreline of all U.S. possessions in the Western Pacific (Johnson Atoll, Kingman Reef, and Palmyra, Wake, Jarvis, Howland and Baker islands) to 200 miles. This area is defined as the U.S. Exclusive Economic Zone (EEZ).

Presently black corals in Hawaiian waters are managed by the State of Hawaii. Fishermen are required to have commercial fishing licenses and report their catch monthly to the Hawaii Division of Aquatic Resources. A state regulation has been drafted which sets a minimum size of 48 inches in colony height and 3/4" in basal diameter for the harvest of *A. dichotoma* and *A. grandis*. At the present time, black coral divers in Hawaii comply voluntarily with this draft regulation.

Precious coral resources within the U.S. EEZ (Fig. 6) are managed by the Western Pacific Regional Fishery Management Council (WESTPAC), under a Fishery Management Plan (FMP) for precious coral (Dep. of Commerce, 1980). The FMP, finalized in September 1983, allows for domestic and foreign fishing by regular or experimental permits and requires logbooks of the permittees. Specific regulations contained in the FMP are as follows:

The FMP and regulations outline and classify the known beds of precious corals within the Western Pacific Region, and designate harvesting method and the amount of corals that can be harvested. There are four bed classifications: 1) Established Beds, 2) Conditional Beds, 3) Refugia Beds, and 4) Exploratory Permit Areas. Established beds are ones with a history of harvest, and optimum yields have been established on the basis of biological stock assessment techniques, and selective harvesting gear (submersibles or remote control harvester vehicles) is required. Makapu'u is the only designated Established Bed. Conditional beds are ones for which yields have been estimated on the basis of bed size relative to established beds with the assumption that ecological conditions at established beds are representative of conditions at all other beds. Four beds are designated as conditional beds: Kea-hole Point, Kaena Point, Brooks Banks, and 180 Fathom Bank. Nonselective harvesting is permitted only in the two conditional beds in the Northwest Hawaiian Islands (Brooks and the 180 Fathom Banks). A refugia bed is one set aside to serve as a baseline study area and possibly reproductive reserve. No harvesting of any kind is permitted in Refugia. Presently, the WESTPAC bed, between Nihoa and Necker Islands, is the only designated Refugia. Exploratory permit areas are unexplored portions of the EEZ in which coral beds are almost certain to exist, but no beds have yet been lo-

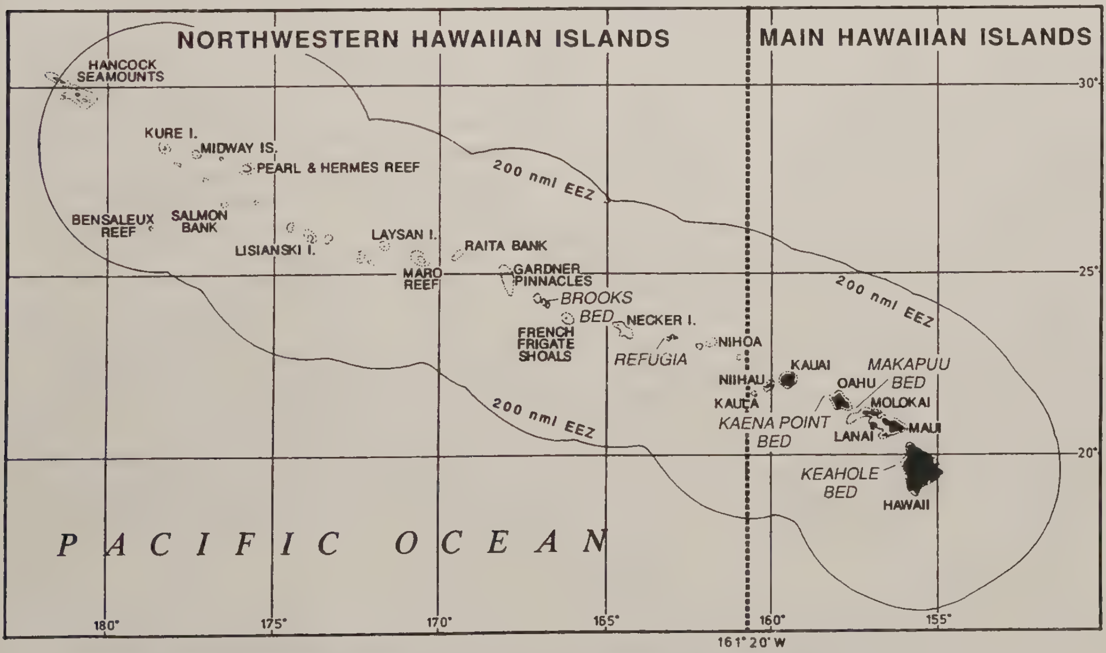
NORTHWESTERN HAWAIIAN ISLANDS
MAIN HAWAIIAN ISLANDS
HANCOCK SEAMOUNTS
KURE I.
MIDWAY IS.
PEARL & HERMES REEF
200 nmi EEZ
BENSALEUX REEF
SALMON BANK
LISIANSKI I.
LAYSAN I.
RAITA BANK
MARO REEF
GARDNER PINNACLES
BROOKS BED
NECKER I.
FRENCH FRIGATE SHOALS
REFUGIA
NIHOA
200 nmi EEZ
KAUAI
MAKAPUU BED
NIIHAU
OAHU
KAULA
MOLOKAI
KAENA POINT BED
LANAI
MAUI
200 nmi EEZ
KEAHOLE BED
HAWAII
PACIFIC OCEAN
30°
25°
20°
180°
175°
170°
165°
160°
155°
161°20'W

Figure 6.—Map of the EEZ in the southern half of the Hawaiian Archipelago showing the location of five precious coral beds.

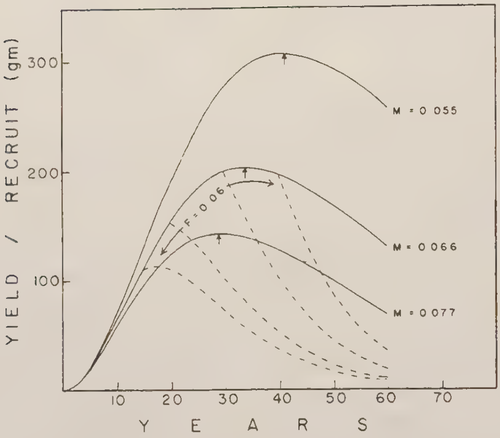

Figure 7.—The Beverton and Holt yield-per-recruit model was used to estimate MSY (vertical arrows) for *Corallium secundum* in the Makapuu coral bed at 3 different values of natural mortality. Dashed lines indicate yield curves produced by applying a fishing mortality of 0.06 at four different ages.

cated. There are four exploratory permit areas; one surrounding the Hawaiian Islands, another that encompasses Guam and the Commonwealth of the Northern Marianas, a third that encircles American Samoa, and a fourth, which was created by Amendment 1 to the FMP, which includes the EEZ's of all the remaining U.S. Pacific Island possessions. Either selective or nonselective harvest gear is permitted in exploratory permit areas except in the Hawaii exploratory area around the Main Hawaiian Islands.

Specific weight quotas and size limits have been determined based on estimates of maximum sustainable yields and optimum yields. For example, the established bed at Makapu'u has a 2-year harvest quota for selective gear only: 2,000 kg for *C. secundum*, 600 kg for *Gerardia* sp. and 500 kg for *L. olapa*. Only colonies of *C. secundum* taller than 10 inches can be harvested. Quotas of 1,000 kg of all species of precious coral combined, exist for each of the EEZ exploratory areas. Foreign fishing is allowed in exploratory areas, if the quotas are not taken by domestic fishermen. Maximum sustainable yields were calculated by using the Beverton and Holt cohort production model (Beverton and Holt, 1957) for *Corallium secundum* (Fig. 2, 7) and the Gulland Model (MSY = 0.4 *M Bo*) where *m* = natural mortality and *Bo* is the virgin biomass, for *Gerardia* and *Lepidisis*.

Having described the management measures established to conserve precious coral resources in Hawaii and the Western Pacific, it is important to evaluate their effectiveness over the history of the fishery. For pink corals, management efforts have been successful for the domestic fishery; however, poaching by foreign fishing has frequently occurred within the U.S. EEZ and is difficult to control.

Considering the domestic coral fisheries first, the cumulative harvest of *Corallium* from the Makapu'u bed between 1966 and 1978 was about 32% of the standing stock. The average annual harvest was 685 kg, somewhat less than the best estimate of MSY, near 1,000 kg. Surveys of the Makapu'u bed in 1983 and again in 1985 showed substantial recovery at rates in close agreement with model predictions in the FMP (Grigg, 1988). For black coral, the combined MSY for beds off Maui and Kauai is 6,250 kg/yr (Grigg, 1976). Harvest levels of black coral above MSY occurred only in the earliest years of the fishery (Table 3) and supply has always been unable to meet demand. Only the most accessible black coral beds off Lahaina, Maui, have been depleted.

Foreign poaching has been a serious problem in the past. During the 1980's, Japanese and Taiwanese coral vessels continuously violated the EEZ near the Hancock Seamounts. In 1985, about 20 Taiwanese coral draggers reportedly poached about 100 tons of *Corallium* from seamounts within the EEZ north of Gardner Pinnacles and Laysan Island. Absence of poaching since that time could indicate that the resources in these areas have been economically exhausted. A research program is currently planned to resurvey the Hancock Seamounts in 1994 with the University of Hawaii research submersible *Pisces V*, in order to assess the present condition of precious coral resources in this area.

## Research Needs and Future Prospects

The most pressing need of the precious coral fishery (and industry) is stock assessment; first in order to describe the status of the stocks within established grounds, and second, to discover new areas. Without substantial efforts to explore and discover new grounds, the precious coral fishery will undoubtedly continue to decline. The problem will become increasingly more serious as existing stockpiles accumulated during the early 1980's are gradually exhausted.

The most promising exploratory areas appear to be in southern oceans. Channel waters around Madagascar and Tasmania (Grigg and Brown, 1991) are particularly promising areas and scattered occurrences of large colonies of *Corallium* spp. have been reported (exact locations are well guarded secrets). Considerable exploration has been conducted in the tropical Pacific by CCOP-SOPAC (Committee for Coordination of Joint Prospecting for Mineral Resources in South Pacific Offshore Areas), and *Corallium* spp. have been recorded from many localities (Cook Islands, Fiji, Kiribati, Solomon Islands, Tonga, Vanuatu, and W. Samoa), but unfortunately not in commercial quality or abundance

(Harper, 1988). Most exploratory dredging by CCOP-SOPAC, however, has been at depths between 200 and 500 m, and virtually nothing is known about the potential of deeper water resources (such as *Corallium* sp. nov. which occurs at a 1,000–1,500 m depth by the Emperor Seamounts).

Another important research question concerns recovery rates (recruitment and growth) in areas which have been heavily harvested. A proposal to assess the stocks on the Hancock Seamounts using the *Pisces V* submersible has been accepted by the Hawaii Undersea Research Laboratory at the University of Hawaii and is presently scheduled for the summer of 1995. The whole area of population dynamics of precious corals is in need of further research.

The mariculture of precious corals is an exciting new area of research. A new laboratory for the biological, economic, and technical research of precious corals has recently been established in Kochi, Japan, in order to attempt the culture of precious coral (Sadao Kosuge, Director of the Institute of Malacology, Tokyo. Personal commun. 1992). To date, colonies of *Corallium japonicum* have been maintained alive in culture for over one year but growth rates are very slow and colonies have not been induced to reproduce. However, the research is still in a very early stage.

While a complete analysis of the economics of the precious coral fishery is beyond the scope of this paper, it is important to mention that this is another area in need of future research. The worldwide glut of *Corallium* precious coral produced during the boom years of the early 1980's caused prices to fall sometimes even below break-even costs for Taiwanese and Japanese coral fishermen and many vessels dropped out of the fishery during this time. The future supply of *Corallium* to the Hawaiian industry will probably continue to depend on exports from these countries; therefore, what happens to the Japanese and Taiwanese fleet is important. Exploration is very expensive and there appears to be little Japanese or Taiwanese interest in wide ranging fishing expeditions at the present time. For this reason, the future of the industry can only be described at this juncture as uncertain. Prices will undoubtedly continue to climb. The raw material for Midway deep-sea coral is still (1990) reasonable at about $150/kg but prices for high quality pink and red *Corallium* peaked in 1990 at $3,069/kg and $16,103/kg, respectively (D. Ancona, U.S. Embassy, Tokyo. Personal commun. 1991). The future of the industry would appear to depend on either successful future exploration or a breakthrough in the mariculture of precious corals.

As for the future of the black coral fishery, at least in Hawaii, it appears to be secure in terms of both supply and demand for the resource. The management of other species of precious coral in Hawaii and the Western Pacific will continue to be covered by the existing FMP of WESTPAC. Regarding the control of foreign fishing in international waters, it is in the best interest of the United States, Japan, and Taiwan to enter into an international treaty for the purpose of conservation of precious corals. However, before this can be achieved, an impetus for such implementation must be initiated by one or all three countries. Based on the principle of common heritage embodied in the International Law of Sea (LOS) convention, and on articles of the LOS Treaty which urge agreements between member countries on measures to conserve living resources within and beyond EEZ's, the Western Pacific Fishery Council has requested that the U.S. State Department enter into multilateral arrangements with Japan and Taiwan for jointly managing the precious coral fisheries in the Pacific.

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# Biology and Management of Deepwater Snappers of the Hawaiian Archipelago

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*ABSTRACT — Commercial and recreational deepwater (100–400 m) bottomfishing in Hawaii targets a multispecies group of lutjanid snappers. Relatively little is known about the life history of these species. Research in Hawaii and elsewhere in the tropical Pacific suggests that most of the species are slow growing, long lived, and have a relatively high age at sexual maturity. Stock assessment is difficult because of the multispecies nature of the fishery. However, recent analysis of commercial fishery data indicates that some of the species may currently be overexploited. Research is underway to determine the efficacy of management measures such as minimum-size limit changes or seasonal and spatial fishery closures to maintain optimal spawning biomass.*

## Introduction

Commercial exploitation of deepwater snappers in Hawaii began before the turn of the century (Cobb, 1903), and except for a hiatus during World War II, has continued to the present. The fishery operates throughout the Hawaiian archipelago, but the inhabited Main Hawaiian Islands (MHI) experience the highest exploitation by both commercial and recreational fishermen. The uninhabited islands and atolls northwest of Niihau, called the Northwestern Hawaiian Islands (NWHI) (Fig. 1), are fished mainly by commercial fishermen.

The deepwater handline fishery targets a multispecies group of fishes consisting of snappers (Lutjanidae), groupers (Serranidae), and jacks (Carangidae). However, snappers are the most important group in the fishery, both by numbers and revenue.[1] Most of the commercially important species have a relatively high age at maturity, long life span, and slow growth rate. These factors, combined with considerable variation in larval recruitment, make these fishes highly susceptible to overfishing. Recent evidence suggests that some of the species may be overfished, and several others are approaching a level of concern[1, 2] (Ralston and Polovina, 1982; Ralston, 1984).

Historically, minimum size limits have been the only measure used to manage both the MHI and NWHI stocks. Since 1989, the NWHI have been managed on a limited entry system. Minimum size limits remain the only management tool currently in effect in the MHI. Several management measures are being evaluated to maintain adequate spawning stock biomass in the future. These include changing minimum size limits, creating closed refuge areas, and imposing bag limits and closed fishing seasons.

This report presents a summary of available information regarding the biology, fishery, and management of these valuable species.

## Species and Distribution

The commercially important deepwater snapper complex in Hawaii is composed of seven species of the lutjanid subfamily Etelinae: *Pristipomoides filamentosus* (opakapaka), *P. seiboldii* (kalekale), *P. zonatus* (gindai), *Etelis carbunculus* (ehu), *E. coruscans* (onaga), *Aprion virescens* (uku), and *Aphareus rutilans* (lehi). Some commercial landings of an introduced snapper, *Lutjanus kasmira* (taape), are also made, but this species usually occurs in shallower water than the other species. The commercially important deepwater lutjanids inhabit the deep slopes of island coasts and banks at depths of 100 to 400 m. These banks and deep slopes comprise an area over 6 times that of shallow water reefs in the state. Biological production in these deepwater areas is thought to be quite different from shallow-water coral reef areas (Agegian et al., 1988).

Throughout their spatial and depth range, deepwater snappers in Hawaii are typically distributed in a clumped pattern, and are often associated with underwater headlands and areas of high relief. Four of the deepwater snapper species found in Hawaii were observed in situ from manned submersibles and an unmanned remotely operated vehicle (ROV) and were found to form large aggregations of up to 100 individuals near submerged promontories and areas of high relief (Brock and Chamberlain, 1968; Ralston et al., 1986; Haight, 1989). This clumped distribution pattern is also apparent when fishing from the surface.

A contributing factor in the distribution pattern of these fish may be that

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[1] (WPRFMC) Western Pacific Regional Fishery Management Council. 1991. Annual bottomfish and seamount groundfish report, 85 p.

[2] S. Ralston and K. E. Kawamoto. 1985. A preliminary analysis of the 1984 size structure of Hawaii's commercial opakapaka landings and a consideration of age at entry and yield per recruit. U. S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Admin. Rep. H-85-1, 9 p.

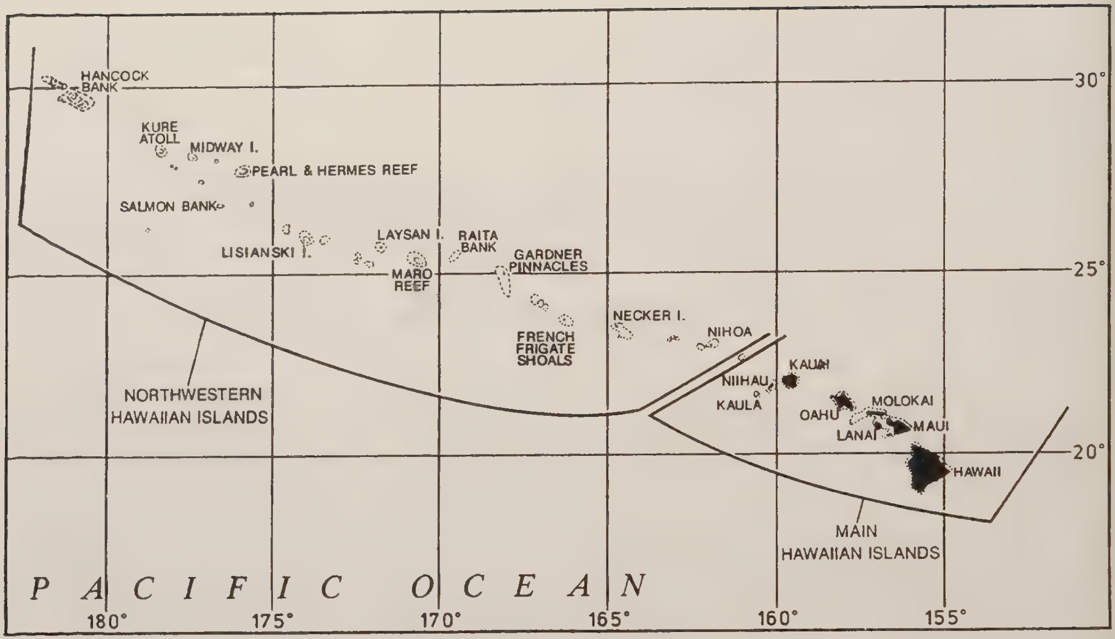

Figure 1. — The Hawaiian Archipelago

currents striking deepwater areas of high relief form localized zones of turbulent vertical water movement, increasing the availability of planktonic prey items (e.g. Brock and Chamberlain, 1968). In an ecological study of the bottomfish resources of Johnston Atoll, Ralston et al. (1986) found *P. filamentosus* in much higher densities on the upcurrent versus the downcurrent side of the atoll, and postulated that this was related to increased availability of allochthonous planktonic prey in the neritic upcurrent areas due to oceanic currents impacting the atoll. Although snappers throughout the world are generally thought of as top level carnivores, several snapper species in the Pacific are known to incorporate significant amounts of zooplankton, often gelatinous urochordates, in their diets (Parrish, 1987). Haight et al. (1993) found zooplankton to be an important prey item in four of the commercially important snappers in Hawaii. The same study found that the six snapper species studied were either primarily zooplanktivorous or primarily piscivorous and showed little overlap in diet composition between trophic guilds.

## Reproduction

Relatively little is known about the reproduction and early life history of deepwater snappers in Hawaii. Size at maturity has been estimated for only two species in the MHI and two species in the NWHI. In the MHI, uku reaches sexual maturity at 47 cm fork length (FL), which is 46% of maximum size ($L\infty$). Onaga reaches sexual maturity at 61 cm FL (62% $L\infty$) (Everson et al., 1989). In the NWHI, ehu reaches maturity at about 30 cm FL (46% $L\infty$) and opakapaka reaches maturity at around 43 cm FL (48% $L\infty$) (Everson, 1984; Kikkawa, 1984; Grimes, 1987).

There is a record of one anecdotal observation on the spawning behavior of opakapaka in Hawaii. A NWHI commercial fisherman using a chromoscope depth sounder observed an opakapaka aggregation at about 150 m become very dense during the mid-morning hours. Catch rates decreased at this time, and egg masses were observed adhering to the fishing gear. By mid-afternoon the school became less compacted and catch rates increased. Opakapaka caught during this time were in spawning condition, some females released eggs and males released milt. Free-floating eggs were noted covering a large surface area around the vessel. The observations were made in mid-April.[3]

Gonadal studies on four of the species in Hawaii indicate that spawning may occur serially over a protracted period but is at a maximum during the summer months, and peaks from July to September (Everson et al., 1989; Uchida and Uchiyama, 1986). Estimated annual fecundity is 0.5 to 1.5 million eggs. The eggs are relatively small (0.7 to 0.8 mm) and are released into the water column.

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[3] (WPRFMC) Western Pacific Regional Fishery Management Council. 1988. 1986 annual report of the fishery management plan for the bottomfish and seamount groundfish fisheries of the western Pacific region, 150 p.

### Larval and Juvenile Stages

Newly hatched larvae of lutjanids in general are typical of those from fish with small pelagic eggs; the larvae have a large yolk sac, unpigmented eyes, and no mouth. The yolk sac typically lasts 3–4 days, after which the mouth is fully formed and the eyes become pigmented (Leis, 1987). The larval stages of snappers in Hawaii are poorly studied, perhaps because of their rarity in plankton samples. In a 16–month survey of the larval fishes near Oahu, snappers of the subfamily Etelinae were taken exclusively in the late summer and fall, and occurred in very low numbers, making up less than 0.5% of the 5,200 fish larvae identified (Clarke, 1991). Snapper larvae are thought to be planktonic and subject to advection by ocean current systems until benthic habitat suitable for metamorphosis is encountered (Munro, 1987). The duration of the pelagic phase is thought to be at least 25 days (Leis, 1987).

Little information currently exists on larval development, settlement, or early juvenile life history of deepwater snappers in Hawaii. Despite considerable research effort directed toward snapper productive processes in Hawaii, little is known about the ecology of juveniles from time of settlement to their appearance in the adult fishery. Age at entry to the fishery for the principal species is thought to be 2 to 3 years after settlement.[4] In a three-year study of fish settlement on artificial reefs adjacent to adult snapper habitat in Hawaii, no recruitment of juvenile snappers to the reefs was observed, although adults aggregated at times around the reef structures (Moffitt et al., 1989).

Occasional reports of recreational fishermen taking juvenile opakapaka while fishing in depths less than 100 m prompted exploratory research fishing to be conducted in these nearshore areas. Results from a 13–month intensive fishing program off Kaneohe Bay, Oahu, Hawaii indicated juvenile opakapaka first appear in the relatively shallow (60–100 m) nearshore areas at about 10 months of age (7–10 cm FL) during the fall and early winter months. The young opakapaka remain in this habitat for the next 7 months until they reach 18–24 cm FL.[5] In situ scuba observations of the juvenile habitat found it to be a relatively flat, soft sediment substrate devoid of relief (Parrish, 1989). Recent trawl surveys suggest juvenile opakapaka are fairly widespread throughout the MHI in similar habitat and depths.[6]

### Age, Growth, and Mortality

Tropical snappers in general are slow growing, long lived, and have low rates of natural mortality. Maximum ages exceed 10 years, and von Bertalanffy growth coefficients ($K$) are usually in the range of 0.10 to 0.25 per year (Manooch, 1987). Most aging studies of tropical snappers have depended on the enumeration of regularly formed marks on calcareous structures. The extended reproductive cycles and weakly expressed seasonality of growth in these fishes, however, confounds the accuracy of such studies. In Hawaii, Ralston and Miyamoto (1983) used daily growth increments deposited on the otoliths of immature *P. filamentosus* to determine its growth rate. Using in vivo tetracycline injection as a validation technique, they concluded that daily otolith increments were deposited in fish up to 3 years old (sexually mature), however, aging of fish greater than age 3 was difficult owing to episodic otolith deposition in sexually mature fish. Based on the growth of immature fish, the estimated growth coefficient of opakapaka was 0.145 per year, and asymptotic upper boundary on growth ($L_\infty$) was 78 cm FL, which occurred at over 18 years of age.

Ralston (1987), in a comprehensive review of published reports on snapper growth and natural mortality, determined that for the 10 species studied, mortality and growth rates were highly correlated, with a mean $M/K$ ratio of 2.0. Thus, if a value of $K$ is available for a given species, its natural mortality rate can be estimated. Using an age-length probability matrix for opakapaka applied to length frequency samples, Ralston (1981) estimated the natural mortality rate for opakapaka in Hawaii to be 0.25, which when compared to the estimated $K$ value for this species (0.145) is close to the value predicted by the $M/K$ relationship derived for snappers in general.

### Fishery Synopsis

Deepwater snapper in Hawaii have been commercially exploited since the early part of the century. In 1925, the Territorial Legislature, concerned with an increasing level of fishing pressure, imposed a one-pound minimum size limit for most of the deepwater snappers. By the 1930's, a fleet of vessels fished for bottomfish throughout the archipelago, with as many as five large (20 m) vessels venturing into the NWHI. After the hiatus imposed on the fishery by WWII, as many as nine vessels fished the NWHI. Landings peaked in the early 1950's at about 500 t, and declined steadily through the mid-1970's (Fig. 2). In the mid-1950's, poor fish prices and vessel losses reduced the number of fishermen in the NWHI; by the 1960's only one vessel remained in operation in the NWHI (Hau, 1984). There was renewed interest in the resources of the NWHI in the mid-1970's when state and federal agencies collaborated in a study focusing on the resources of this region. Bottomfish resources within this area were investigated during conducting an economic study of the fishery. The potential of the NWHI bottomfish resource prompted many new fishers to enter the fishery.

During the late 1970's, the fleet exploited banks closest to the MHI ports. As yields decreased, the fleet moved farther into the NWHI. A few vessels with extended fuel and hold capacity

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[4] S. Ralston and K. E. Kawamoto. 1987. An assessment and description of the status of bottom fish stocks in Hawaii. U. S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent. Admin. Rep. H-87–7, 55 p.

[5] R. B. Moffit and F. A. Parrish. In review. Temporal and spatial utilization of habitat by juvenile Hawaiian pink snapper, *Pristipomoides filamentosus*.

[6] D. A. Ellis, E. E. Demartini, and R. B. Moffitt. 1992. Bottom trawl catches of juvenile opakapaka, *Pristipomoides filamentosus* (F. Lutjanidae), and associated fishes, Townsend Cromwell cruise TC-90–10, 1990. U. S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent. Admin. Rep. H-92–03, 33 p.

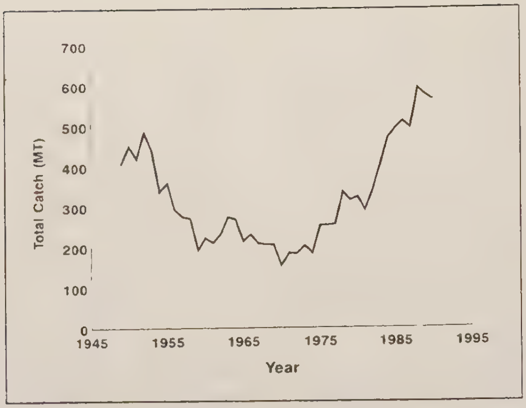

Figure 2. — Annual commercial bottomfish landings for the entire Hawaiian Archipelago, 1948–1990. (State of Hawaii, Division of Aquatic Resources data)

were fishing around Midway and Kure by 1988. The fishery expanded rapidly in the 1980's and landings peaked in 1987 (Fig. 2). Increased fishing pressure and fluctuating exploitation rates in the NWHI prompted the Western Pacific Regional Fishery Management Council (WPRFMC) to impose a limited access system for a large part of this area in 1989. Currently, effort in the portion of the NWHI west of Necker Island (Fig. 1 ) is limited to 6 vessels.

### Fishing Gear

The Hawaiian snapper fishery utilizes various modifications of traditional Hawaiian handline gear. The gear consists of a main line with a 2–4 kg weight attached at the terminus. Several 40–60 cm sidelines with circle hooks are attached above the weight at 1 m intervals. The basic design of the handline gear used in the fishery has remained essentially unchanged from gear used by early, indigenous Hawaiians.

Commercial snapper fishermen in Hawaii mainly utilize vessels 10–20 m in length. The vessels are usually equipped with color video depth and fish echo sounders, satellite navigation receivers, Single Side Band (SSB) and VHF radios, EPIRB's, and hydraulic line-pulling equipment.

Vessels venturing into the NWHI tend to be in the upper end of the size range, as distance from ports and lack of rough-weather shelter keep many of the smaller vessels closer to their home ports. The MHI vessels, although smaller than those used in the NWHI, are similarly equipped.

There are also many part-time recreational/commercial fishermen in the MHI. The boats involved in this fishery are smaller than the full-time commercial vessels and usually range from 5 to 15 m in length. Most of the part-time fishermen have color video depth/fish sounders, CB radios, and electric line-pulling equipment. Many also have satellite navigation equipment.

Since the late 1960's, the availability of improved navigational and fishing gear has greatly increased the fishing power of both commercial and recreational fishermen in Hawaii. It is now possible to return to a particular fishing spot with great accuracy in various weather conditions using electronic navigation equipment and to target single species using color video sounding equipment. In the past, triangulation from visible onshore landmarks was the most common method of relocating productive fishing grounds. This method can be very accurate, but depends on weather and other conditions beyond the control of the fisherman.

Until recently, many fishermen targeted individual species of snappers, but this strategy is not commonly practiced today. Most fishermen now diversify fishing effort because of decreased catch rates for some of the species. Targeting different species of snapper seasonally, or fishing for pelagic species when bottomfish are scarce, is now commonly practiced.

### Seasons and Markets

The various snapper species are mainly caught during the months of November–February, with peak catches in December. Uku is an exception in that it is heavily exploited during the summer months when it aggregates in shallow water to spawn. Some uku are landed incidentally in December owing to increased fishing pressure on opakapaka which occurs at the same depths as uku.

A large portion of the MHI snapper landings is taken by recreational fishermen; therefore, the NWHI commercial fishery plays an important role in providing a consistent supply of fresh bottomfish to local markets. Generally the demand for fresh fish outstrips the supply. Snapper from various Pacific island nations are imported at times to supplement the supply of local fish. In the past these imports generally were of lower relative quality; however, in recent years the quality of these imports has improved dramatically. The price of these imported fish has also increased but is still lower than that of comparable local fish. The seasonal abundance of these imports can affect the price of the local bottomfish. However, most imports occur during the local low season for bottomfishing, which contributes to a year-round consistent supply of fish.

Most commercial fish in Hawaii are sold at wholesale fish auction houses. The demand for freshness and quality is high. Ex-vessel price can vary considerably depending on the quality of individual lots of fish. Snappers are generally separated into two categories at the auction: 1) large fish for the restaurant fillet market and 2) smaller whole fish for local consumers. Demand from local tourist-oriented restaurants is the major factor in bottomfish market economics. The local consumer market for smaller fish fluctuates to some extent, with peak demand occurring during traditional winter holidays.

## Fishery Data Collection

In Hawaii, fishermen who sell all or part of their catch must be commercially licensed and submit a monthly catch report. These data have been available from the State of Hawaii Division of Aquatic resources (HDAR) since 1948. In the MHI, incomplete reporting, and the "under-the-table" selling of fish by recreational fishermen confound the accuracy of the catch reporting system. In 1984 the WPRFMC initiated a monitoring program at the Honolulu fish auction to provide additional information on bottomfish landings in Hawaii. In 1986 the NMFS assumed responsibility for the program. In 1990, the HDAR began to share monitoring duties with the NMFS on a half-time basis. During the years 1984 through 1987, monitoring was conducted six days per week. This was reduced to five days per week in 1988, and three days per week in 1992. Information collected includes name of vessel or fisherman, date of sale, general area fished, species of fish, number of fish and corresponding weight, price per pound, and buyer. Information is recorded on a data sheet, coded and keypunched for analysis. Until recently, the majority of snapper sold in Hawaii passed through the monitored site. However, beginning in 1991, the majority of NWHI landings were not sold at the monitored site, which increased the difficulty in monitoring total archipelago landings.

An additional problem in obtaining total archipelago catch information is the large number of fish landed by recreational fishermen and not reported. The MHI recreational catch of snapper is impossible to accurately estimate. The large number of small trailerable boats currently registered in Hawaii gives an indication of the magnitude of the problem. Many of these "recreational" fishermen often sell their catch disregarding commercial fishing license requirements. The ease of selling privately to wholesalers, retail fishmarkets, restaurants, supermarkets, peddling, etc., without the proper licenses or reporting, leads to serious underestimation of total state catches.

## Stock Status and Population Dynamics

Several different stock assessment approaches have been applied to the Hawaiian deepwater snapper fishery. These will be reviewed in approximate order of methodological complexity, which is similar to their chronological order in time because of developments in stock assessment methods and/or availability of additional data.

Simple catch per unit of fishing effort (CPUE) of commercial fishermen or research vessel surveys is commonly used as an index of stock abundance. CPUE alone can only provide estimates of relative changes in abundance; but, when coupled with certain assumptions and cast in the proper mathematical framework, it is possible to obtain measures of absolute abundance by estimating a catchability parameter. Catchability can be estimated in several different ways, and one of the more common approaches is to use the catch data in a surplus production model which will also estimate other fishery statistics such as maximum sustainable yield. Ralston and Polovina (1982) used a Schaefer surplus production model in one of the earliest attempts to assess MHI deepwater snapper stocks. The parameters for this model were estimated from a linear regression of yearly CPUE on yearly effort over the time period 1959–1978 (HDAR data). Rather than fit individual models to each species, Ralston and Polovina found that an intermediate level of species aggregation (from the species pool of 8 deepwater snappers) resulted in significantly improved fits to the model. This was apparently due to both depth segregation by species and the multispecies nature of the fishery where, since fishing effort (in fisherman-days) is not necessarily directed at a single species, single species CPUE, calculated by using the aggregate fishing effort, does not reflect that species abundance. Ralston and Polovina sought to aggregate species in the analysis to essentially mimic the aggregate nature of the fishing effort. This optimal level of species aggregation was objectively determined through cluster analysis of species weight composition in HDAR daily commercial catch reports. The potentially complex effects of interaggregation interaction (i.e. predation, competition, and mutualism) were statistically examined and dismissed. Of the four MHI regions examined, statistically significant models were consistently achieved only for the Maui-Lanai-Kahoolawe-Molokai (MLKM) region (Fig. 1), an area which accounts for over 50% of the statewide bottomfish landings. This provided an estimate of MSY per habitat area which was then used in conjunction with other habitat area estimates to extrapolate other regional and total MSY's in the MHI and NWHI. Ralston and Polovina concluded that the MHI aggregate bottomfishery was operating at or near MSY in 1978, and in more recent years both MHI and NWHI landings have consistently exceeded estimates of MSY[4,7] (Polovina, 1987), a situation difficult to interpret for purposes of stock assessment. The next level of stock assessment approaches for Hawaiian deepwater snappers attempted to utilize information on age and growth and patterns of size/age at entry to the fishery on a species-specific level.

Assessment of Hawaiian deepwater snappers in the 1980's relied heavily on the Beverton and Holt (1957) approach, also referred to as dynamic pool modelling. The normal methodology is simply to use the equations presented by Beverton and Holt (1957), inserting where necessary the von Bertalanffy growth coefficient ($K$) or asymptotic length ($L\infty$) parameters, values of total, natural, or fishing instantaneous mortality ($Z$, $M$, or $F$), and ages at maturity or entry to the fishery ($t_m$ or $t_e$). Since this complete set of information is not available for many species of Hawaiian deepwater snappers, alternative methods must often be used to solve the yield equation.

The first alternative method is to estimate independently as many parameters as are within the limits of the

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[7] S. Ralston and K. E. Kawamoto. 1988. A biological assessment of Hawaiian bottom fish stocks, 1984–87. U. S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent. Admin. Rep. H-88-8, Honolulu, Hawaii, 60 p.

database, and then use empirical relationships to estimate the remaining parameters. Ralston and Kawamoto[7] used this approach for five species of Hawaiian bottomfish (including four species of deepwater snappers: ehu, onaga, opakapaka, and uku), starting with estimates of $L\infty$ and the ratio $Z/K$ from application of the Wetherall et al. (1987) method on catch length frequencies. These length frequencies were converted from Honolulu auction weight data by using the length-weight conversion parameters from Loubens (1980), Uchiyama et al. (1984), Brouard and Grandperrin (1984), and Ralston (1988). The empirical relationship presented in Manooch (1987) was used to estimate $K$ from $L\infty$, and the empirical relationship presented in Ralston (1987) was used to estimate $M$ from $K$. The mortality parameters $Z$ and $F$ were deduced algebraically, where $Z=(Z/K)K$ and $F=Z-M$. Ages at entry were estimated from the ascending limbs of the weight frequency distributions, by using the length-weight conversion parameters and $L\infty$ and $K$ (assuming $T_0=0$). The estimates of $L\infty$ and $K$ were further used to construct a length converted catch curve from the length frequency distributions (also assuming $T_0=0$), resulting in another estimate of $Z$. Ralston (1984) also estimated M from $L\infty$, $K$, and water temperature using the empirical formula given in Pauly (1980). Generally, multiple estimates of a parameter were averaged when they were in close agreement. Ralston and Kawamoto[7] concluded that NWHI stocks were healthy, but most MHI stocks were being growth overfished by excessive harvesting of juvenile fish. They recommended some form of management regulation to counteract this.

The second alternative method is to modify the yield equation to a form which uses the ratios $Z/K$, $M/K$, or $F/K$ rather than $Z$, $M$, $F$, or $K$ since the former are readily calculable by using the Wetherall et al. method on weight-converted length frequency samples from a fished population (where $Z/K=M/K+F/K$) and an unfished population (where $Z/K=M/K$). $F/K$ can then be solved for by subtraction, $F/K=Z/K-F/K$. This was suggested by Polovina (1987) and implemented by Somerton and Kobayashi[8] to calculate the spawning potential ratio (*SPR*=ratio of current spawning stock biomass per recruit to the virgin spawning stock biomass per recruit) for two species of MHI deepwater snappers (ehu and opakapaka). This analysis assumed that length frequencies of NWHI catch approximated a virgin unfished condition. Somerton and Kobayashi[8] concluded that *SPR* values were in the 20–30% range which borders on the 20% value generally accepted as an indicator of recruitment overfishing (Beddington and Cooke[9]).

Both of these ad hoc applications of Beverton-Holt probably suffer from biases because of the variety of approximations and assumptions. One bias potentially affecting both approaches is due to use of the Wetherall et al. method to estimate initial parameters of the analyses. Somerton and Kobayashi (1991) used computer simulation to show that estimates of $Z/K$ and $L\infty$ from the Wetherall et al. method can be either positively or negatively biased for many years while the population is adjusting to a change in fishing intensity or from a recruitment perturbation (however, bias due to recruitment seasonality per se can be negligible [Ralston, 1990]). Even under equilibrium conditions there can be substantial bias due to error in estimating the size at complete fishery selection and growth variability (Somerton and Kobayashi, 1991; Issac, 1990). In their assessment of the 1988 bottomfish stock, Somerton et al.[10] abandoned the Beverton-Holt approach because of uncertainties regarding this type of bias; however, as mentioned previously, Somerton and Kobayashi[8] applied the $Z/K$, $M/K$, $F/K$ version of Beverton-Holt to estimate *SPR* for ehu, which does appear to be in equilibrium, and for opakapaka, for which there are additional data on size at complete fishery selection.

Ralston and his coworkers[2,4,7] (Ralston, 1981, 1984; Ralston and Miyamoto, 1983) have assembled an extensive database on the biology and fishery for opakapaka, which is by far the single best known species of Hawaiian deepwater snapper. For this reason, assessment approaches for opakapaka require fewer assumptions and approximations, and often there are multiple estimates available for a desired parameter. Ralston (1984) and Ralston and Kawamoto[2] applied yield-per-recruit analyses to opakapaka which made use of many independently estimated parameters. Von Bertalanffy parameters were obtained from a study of otolith microstructure (Ralston and Miyamoto, 1983), and $Z$ and $M$ were estimated from length converted catch curves from fished and unfished areas, and age at entry was estimated from the ascending limbs of catch weight frequency distributions, by using length-weight conversion and von Bertalanffy parameters.

Somerton and Kobayashi[8] developed a computationally simple dynamic estimator of *SPR* that makes use of a time series of CPUE and catch size frequencies. Assuming that CPUE is an index of population size, changes in CPUE over time, coupled with the changes in the catch size composition, can be used to make estimates of *SPR*. Resorting to a similar strategy as that of Ralston and Polovina (1982), Somerton and Kobayashi[8] aggregated species in the CPUE index and were able to calculate species-specific dynamic *SPR* for five MHI bottomfish species (including four species of deepwater snappers: ehu, onaga, opakapaka, and uku) by utilizing species-specific catch size frequency distributions and sizes at maturity. These dynamic *SPR* values were similar to the equilibrium SPR values, falling in the range of 20–40%. The earliest

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[8] D. A. Somerton and D. R. Kobayashi. 1990. A measure of overfishing and its application on Hawaiian bottomfishes. U. S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent. Admin. Rep. H-90–10, 18 p.

[9] J. R. Beddington and J. G. Cooke. 1983. The potential yield of fish stocks. FAO Fish. Tech. Pap. 242, 47 p.

[10] D. A. Somerton, B. S. Kikkawa, and A. R. Everson. 1989. Biological assessment of the Hawaii bottom fish stocks and the southeast Hancock Seamount armorhead stock, 1988. U. S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent. Admin. Rep. H-89–6, 34 p.

(1948) CPUE data were considered virgin, but it is known that considerable bottomfishing may have been taking place at least as early as the 1930's (Polovina, 1987); and no attempt was made to correct for technological improvement in fishing efficiency. Clearly, there is a need for some type of dynamic stock estimator which does not rely on CPUE.

The logical alternatives are dynamic production modelling or age-structured models. The former approach is handicapped by incomplete landings and effort data, and the lack of a reliable CPUE. The latter approach may be more suitable, particularly since more age and growth data are available from ongoing otolith studies. Preliminary application of stock-synthesis, an age-structured model developed by Methot (1989, 1990), to NWHI opakapaka has been favorable[11], and a synthesis-like equilibrium approach called IMMAGE (Somerton and Kobayashi, 1992) has been successfully used to estimate recruitment, fishing mortality, and the gear selection curve for MHI and NWHI opakapaka[11]. Currently, the 1991 stocks are assessed with the CPUE-based dynamic *SPR* method.

### Management and Regulation

Current fishing regulations for Hawaiian deepwater snappers include commercial minimum size limits of 1 pound for opakapaka, onaga and uku, and limited entry in the NWHI. There are no bag limits, closed seasons, or recreational minimum size limits for any deepwater snapper.

Somerton and Kobayashi[12, 13] explored the possible consequences of increasing the minimum size limit for opakapaka from 1 to 3 pounds or initiating a 1–3 month seasonal closure of the fishery. Their results from computer simulation indicated that both management strategies could substantially benefit the fish population in terms of increasing the spawning stock biomass. The potential increases ranged from 15–300% after a time period of 5–10 years, depending on the initial condition of the stock. Maximal benefits are attained if sublegal fishing mortality is minimal (i.e. small fish are avoided or released alive) in the case of a size limit increase, and if a seasonal closure effectively reduces the total annual fishing mortality (i.e. there is no compensatory increase in fishing effort during the open season). It is unlikely that the long-term equilibrium yield would increase; however, the population would be less vulnerable to recruitment overfishing and the associated catastrophic stock decline. The State of Hawaii is currently evaluating these and other management options (e.g. bag limits, areal closures) in response to concerns of deepwater snapper overfishing, primarily in the MHI.

### Research Needs Pertaining to Management

Details of the reproductive biology are minimally adequate for most of the primary Hawaiian deepwater snapper species. More age and growth studies are needed, particularly for the younger and smaller fish, with enough data to better define the magnitude of growth variability. Discrepancies in growth estimation due to methodological differences in aging (e.g. Morales-Nin and Ralston, 1990; Radtke, 1987; Smith and Kostlan, 1991) need to be addressed and resolved, as this information forms the foundation for cohort/virtual population analysis, or stock synthesis assessment models. Movement patterns of adults and the extent of egg and larval dispersal need further study to clarify the identity of individual stocks, which would help determine the temporal and spatial scale for effective management.

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[12] D. A. Somerton, and D. R. Kobayashi. 1990. Some effects of increasing the minimum commercial size limit of opakapaka, *Pristipomoides filamentosus*. U. S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent. Admin. Rep. H-90–3, 10 p.

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# Feeding Ecology of Deepwater Lutjanid Snappers at Penguin Bank, Hawaii

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*Abstract.*—Deepwater snappers are a valuable component of fisheries on slopes and banks in Hawaii and in much of the world's tropics. Their ecology and trophic relationships in these deepwater habitats are poorly known. Line fishing in this study simultaneously collected six of the seven lutjanid species that commonly occur in the major deepwater snapper fishery at Penguin Bank, Hawaii. The catch rate of each species showed diel variability; the patterns of some species were distinctly different. The depth distribution of feeding, as indicated by depth of capture, differed considerably among species; all species were taken within several meters of the bottom. Size (fork length) of the predator species did not appear to be stratified by time of capture (daylight versus darkness) or median capture depth. Regurgitation of gut contents seemed to be reduced when fish were retrieved at a rate that was slower than used in commercial practice but rapid enough to prevent death or morbidity while hooked. The food remaining in line-caught specimens appeared to be representative of what was originally eaten. The six snapper species ate considerable amounts of a wide range of pelagic animals and demersal fishes and much smaller quantities of a few invertebrate benthic groups. *Etelis coruscans*, *Etelis carbunculus*, and *Aprion virescens* formed a distinct, primarily piscivorous feeding guild. *Pristipomoides filamentosus* and *Pristipomoides sieboldii* formed a distinct guild dominated by zooplankton feeding. The few specimens of *Pristipomoides zonatus* appeared somewhat intermediate in diet. Important planktonic prey groups included crustaceans, pteropods, and large, pelagic, colonial urochordates (e.g., salps). Urochordates made a significant contribution to the diet even for some of the primarily piscivorous species. Major diel and seasonal shifts in diet were found only in *P. filamentosus*; they involved the relative proportions of fish, and especially of the major planktonic groups. Our information on diet composition and depth and time of feeding (catch) suggests that considerable resource partitioning occurs among these deepwater snappers.

Deepwater lutjanid snappers represent an important resource throughout the tropical and subtropical oceans of the world. Many species of Lutjanidae are highly prized as food fish and typically have a high market value wherever they are found (Polovina and Ralston 1987). In the tropical Pacific, several genera of these fishes inhabit the slopes of land masses and banks at depths of 100–400 m. Understanding the trophic support for these fishes in this environment can provide important insight for management of their fisheries. Published studies of the diets of deepwater snappers are scarce, however, because these fisheries occur in isolated locations, and collecting gut contents from such deepwater fishes is difficult (Parrish 1987).

In Hawaii, deepwater lutjanid snappers are the mainstay of the commercial and recreational bottom fish fishery, contributing over 88% by weight and 93% by value of the total commercial deepwater bottom fish landings in 1990 (HDAR 1991). Bottom fishing is mainly concentrated on the steep slopes of deepwater banks. These banks and the deep slopes of island coasts have an aggregate area over six times that of shallow-water reefs in the state (Agegian et al. 1988). Similar grounds support existing or potential snapper fisheries in much of the Pacific and other tropical waters (Polovina and Shomura 1990). Our limited understanding of the ecology and production of deepwater banks suggests that these important habitats probably function very differently from shallow-water coral reef ecosystems. The interaction between currents, the daily tidal regime, and the physical structure

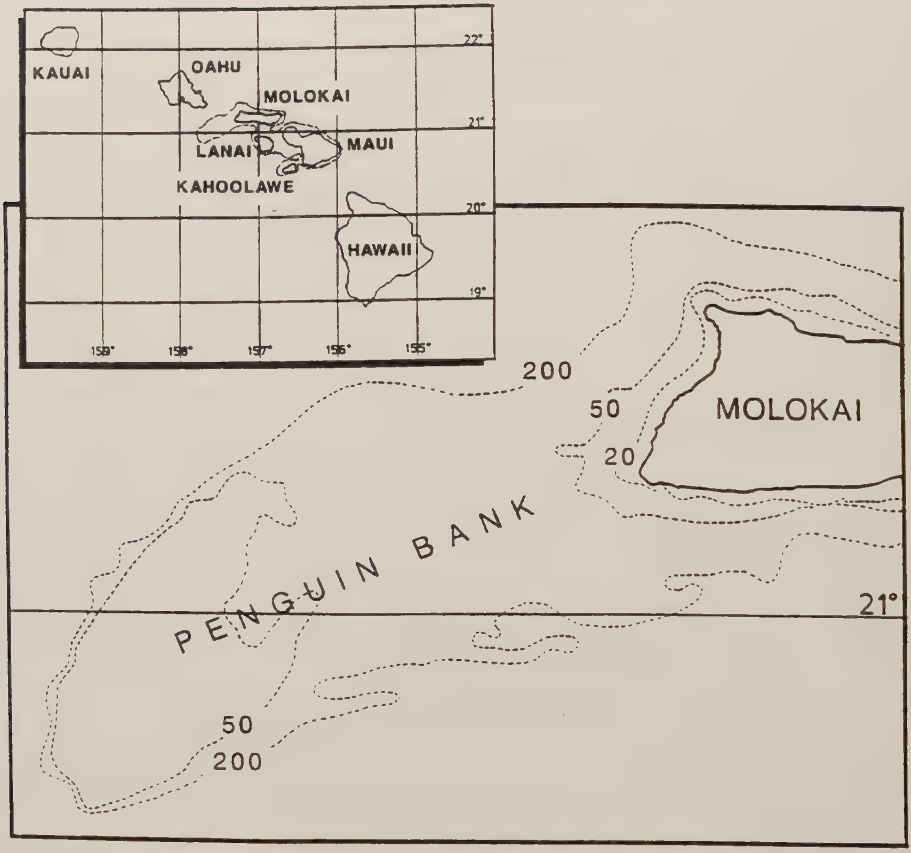

FIGURE 1.—Penguin Bank and immediate surroundings in the Hawaiian Archipelago. Bathymetric contours are in meters. The Molokai–Lanai–Kahoolawe–Maui bank complex is indicated generally by the bathymetric contour (200 m) in the inset.

of the banks may produce hydrographic features that are distinctive and have different effects on system productivity (Agegian et al. 1988).

The Molokai–Lanai–Kahoolawe–Maui bank complex (Figure 1), of which Penguin Bank is a large part, produces about 41% of the commercial bottom fish catch of the main Hawaiian Islands (based on 1990 landings statistics from the Hawaii Division of Aquatic Resources). In addition, there is a large but unrecorded recreational catch (Ralston and Polovina 1982; WPRFMC 1986). After recent heavy fishing pressure, there are indications that some stocks on these banks have been overfished and are declining (Ralston and Polovina 1982; Ralston 1984; Ralston and Kawamoto 1985, 1988; HDLNR 1986; WPRFMC 1986, 1988). Knowledge of these stocks is based almost entirely on data from landings by the commercial handline fishery. Some information is available on basic life history characteristics (e.g., growth parameters, reproductive data, size data, and mortality rates) of some major species in the fishery (Ralston 1981; Everson 1984; Kikkawa 1984; Kikkawa and Everson 1984; Uchiyama et al. 1984; Uchiyama and Tagami 1984; Sudekum et al. 1991). However, little is known about the habitat, food resources for bottom fish, or other characteristics of the environment that make it a productive fishing ground.

Except for some data on the diet of the greater amberjack *Seriola dumerili* (Humphreys and Kramer 1984), almost nothing is known about the feeding ecology of the commercial bottom fishes at Penguin Bank. Trophic information for these species from other localities also is sparse. One jack species (*Pseudocaranx dentex*) has been studied by Seki (1984a), two snapper species (*Pristipomoides auricilla* and *Pristipomoides zonatus*) by Seki and Callahan (1988), and two other jacks (giant trevally *Caranx ignobilis* and bluefin trevally *Caranx melampygus*) by Sudekum et al. (1991). All available diet information on deepwater groupers and snappers has been surveyed by Parrish (1987), including results from elsewhere in the Hawaiian Archipelago obtained by Kluegel (1921) and Seki (1984b) and previously unpublished results on diets of fishes from the Northwestern Hawaiian Islands (NWHI) and the Marianas.

The overall goal of our study was to identify and characterize key relationships between commercially important deepwater bottom fishes and their habitats and major food sources. Specific objectives were (1) to determine whether there is overlap among deepwater lutjanid snappers in their depth ranges or feeding periods, (2) to identify important prey groups in the diets of these species and estimate their relative importances, (3) to determine the extent of overlap in diet for these predators, and (4) to identify any diel or seasonal shifts in their diets.

## Study Area

Penguin Bank is a large underwater feature immediately southwest of the island of Molokai, Hawaii (Figure 1). The top is relatively flat, with depths of 50–100 m; at the periphery, the bathymetry drops rapidly to over 500 m (Gregory and Kroenke 1982). Penguin Bank is similar in depth to the other banks in the Hawaiian Archipelago, and production dynamics on Penguin Bank are probably representative of many such banks in Hawaii and elsewhere in the tropics. Suitable habitat for bottom fish seems to be limited to a small and rather scattered fraction of the entire Penguin Bank area (C. R. Agegian, University of Hawaii, J. J. Polovina, Honolulu Laboratory, National Marine Fisheries Service, and S. Ralston, Tiburon Laboratory, National Marine Fisheries Service, personal communications).

## Methods

*Specimen collection.*—Several areas of Penguin Bank known as commercially productive fishing grounds were chosen for specimen collection. These sites were surveyed hydroacoustically with a Raytheon model LSR-910M and a Simrad type EQ38-MK3 paper-recording fathometer, a RD Instruments series RDVM acoustic doppler current profiler, and a Furuno model CN106 color chromoscope.[1] Information was collected on bathymetry, substrate type, and fish aggregations. Some nearby areas on top of the bank also were fished to obtain adequate diet samples from the snapper *Aprion virescens*.

Specimens were collected between October 1987 and December 1989, primarily by conventional bottom handlines deployed from hydraulic fishing gurdies (Uchida and Uchiyama 1986:29). Five stations were fished with a Kali bottom longline developed at the National Marine Fisheries Service's Honolulu Laboratory (Shiota 1987). The use of rigid polyvinylchloride tubing in this gear in place of conventional gangions or dropper lines greatly reduced problems with fouling on the rough bottom. Stripped squid was used for bait for all handlining and longlining. All hooks were fished within a few meters of the bottom.

A handline fishing station consisted of a series of drifts made over a selected site after wind and current directions were determined. Drifts varied in response to local conditions and topography, but a typical station was occupied 1–3 h, during which time sampling occurred at depths ranging from about 100 to 250 m. An effort was made to sample the complete depth range fairly evenly throughout the diel cycle. Total fishing effort was 248 line-hours during daylight (0600–1830 hours) and 294 line-hours during darkness (1830–0600 hours). The shallow (0–150 m) and deep (150–300 m) depth ranges were each fished at least 90 line-hours during each period (daylight and darkness). In the standardized fishing, each 50-m depth interval from 50 to 300 m was handlined for a minimum of 25 line-hours. At least 20 line-hours of effort were exerted in each 2-h time interval throughout the diel cycle (Table 1). Effort was not equal for various times of day and depths, so most catch data were expressed as handline catch per unit effort (CPUE).

To determine if there were species-specific patterns of temporal and spatial distribution, the handline catch of each species, expressed as a fraction of the total handline catch of all species, was compared by chi square analysis ($\chi^2$) to a uniform distribution of expected (equal) catch of all species. This procedure was used separately for each 2-h interval of the day and for each 50-m interval of depth fished.

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[1] Mention of products or names of manufacturers does not imply endorsement by the U.S. Government.

Because regurgitation of gut contents is a problem when line-caught fish are brought to the surface rapidly by commercial fishing methods, various decompression schedules were tested. Lines were retrieved at different rates, and the general condition of each fish and the extent to which it had regurgitated were recorded. The most visible sign of barotrauma was the eversion of the stomach forward through the esophagus, caused by the expansion of gas in the swim bladder. To quantify the potential for loss of gut contents by regurgitation, each fish was assigned an integral value (ranging from 0 to 4) reflecting the degree of extrusion of the stomach into the mouth cavity. Time, depth, and location of capture, rate of ascent, and regurgitation state value were recorded for each specimen. The mouth and gills were examined for regurgitated material (which was included in diet analysis), and the specimen was weighed (to the nearest 0.01 kg), measured (standard length, fork length, and total length to the nearest 1 mm) and sexed (by macroscopic appearance of gonads after dissection). Fish were cooled quickly, and within 1 h after capture, the gastrointestinal tract was removed and frozen. Altogether, 589 fish were collected. All identifiable prey items from 219 of these predator specimens were used in trophic analysis.

*Trophic analysis.*—Diet composition was determined by examining the contents of the entire gastrointestinal tract of each specimen, following procedures similar to those described in Hyslop (1980), Harrison et al. (1983), and Parrish et al. (1985). All prey organisms were identified visually under magnification to the lowest feasible taxon. All prey individuals were counted, and the volume of individuals or groups of individuals was measured by liquid displacement. If a prey individual was in an advanced state of digestion, its volume was estimated by comparing it with intact individuals of similar size and known volume. Parts of partially digested prey were measured (e.g., with an ocular micrometer) to permit estimates of the sizes of the intact individuals.

TABLE 1.—Distribution of total standardized handline fishing effort applied simultaneously for six snapper species collected at Penguin Bank, Hawaii, in 1987–1989.

| Effort distribution by time of day | | Effort distribution by depth | |
|---|---|---|---|
| Time of day (hours) | Effort (line-hours) | Bottom depth (m) | Effort (line-hours) |
| 0000–0200 | 27.8 | 50–100 | 25.4 |
| 0200–0400 | 20.2 | 100–150 | 188.8 |
| 0400–0600 | 29.1 | 150–200 | 188.9 |
| 0600–0800 | 41.9 | 200–250 | 110.1 |
| 0800–1000 | 37.8 | >250 | 28.0 |
| 1000–1200 | 54.3 | | |
| 1200–1400 | 37.4 | | |
| 1400–1600 | 32.6 | | |
| 1600–1800 | 43.0 | | |
| 1800–2000 | 62.0 | | |
| 2000–2200 | 128.8 | | |
| 2200–2400 | 27.4 | | |

Diet composition was expressed in terms of number and volume of prey items and frequency of occurrence of predator guts containing the prey. An index of relative importance (IRI) for each prey category in the diet was calculated with the method of Pinkas et al. (1971):

$$\mathrm{IRI} = F(N + V);$$

$F$ = percentage of all predator individuals that contained that prey category,

$N$ = percentage of total prey individuals that were of that category, and

$V$ = percentage of total prey volume that was of that category.

To compare diets, the IRI of a particular prey category was expressed as a fraction of the sum of IRI values for all categories at comparable levels of systematic or ecological organization.

Diet overlap between predator groups was calculated by the Morisita–Horn $C_\lambda$ formula (Horn 1966):

$$C_\lambda = \frac{2\sum_{i=1}^{s}(x_i y_i)}{\sum_{i=1}^{s} x_i^2 + \sum_{i=1}^{s} y_i^2};$$

$s$ is the total number of prey categories, and $x_i$ and $y_i$ are the proportions of the total diet index of predator group $x$ and $y$ that are taken from prey category $i$. Values of $C_\lambda$ can vary from 0 when diets of two groups are completely distinct to 1 when the diets are identical. Diet overlaps were classified with Langton's (1982) scale: low overlap, 0–0.29; medium overlap, 0.30–0.59; and high overlap, ≥0.60. Groups compared for diet overlap included different predator species, predators collected in different seasons and at different times of day, and different portions of the alimentary tract (i.e., stomach, mouth and hindgut).

TABLE 2.—Six deepwater snapper species collected in this study, by number and size caught, time of day, and depth of capture, at Penguin Bank, Hawaii, in 1987–1989.

| Species | Number collected | Fork length (mm) |  | Time of day caught (hours) | Depth of capture (m) |  |
|---|---|---|---|---|---|---|
|  |  | Range | Median |  | Range | Median |
| *Pristipomoides sieboldii* | 147 | 237–435 | 363 | 0036–2242 | 104–265 | 168 |
| *Pristipomoides filamentosus* | 232 | 267–654 | 388 | 0010–2348 | 49–256 | 107 |
| *Pristipomoides zonatus* | 7 | 322–410 | 387 | 0915–1806 | 150–190 | 164 |
| *Etelis coruscans* | 40 | 265–836 | 404 | 0540–1905 | 163–331 | 192 |
| *Etelis carbunculus* | 92 | 232–576 | 346 | 0150–2258 | 73–280 | 175 |
| *Aprion virescens* | 71 | 443–890 | 633 | 0615–1850 | 46–134 | 51 |
| Total | 589 |  |  |  |  |  |

Statistical analyses were done on a microcomputer with the software package SAS PC Release 6.03 (SAS Institute 1985, 1988).

## Results

### *Catch Composition*

Six of the eight native lutjanid snapper species known from Penguin Bank were captured in this study (Table 2). The only common, native, deepwater lutjanid of this habitat not present in the catch was *Aphareus rutilans*.

*Pristipomoides sieboldii* and *Pristipomoides filamentosus* made up 64% of the catch; *P. zonatus* was caught only incidentally (1%). *Etelis coruscans* and *Etelis carbunculus* made up 23% of the catch. *Aprion virescens*, an important commercial species in summer, accounted for 12% of the total.

### *Spatial and Temporal Distribution of the Catch*

The distribution of depths and times of catch of most of the six snapper species overlapped somewhat, but some distinct species differences were discernible. *Pristipomoides filamentosus* seemed to take bait most readily during the morning (0400–0800 hours) and evening (1600–2200 hours) (Figure 2A). *Pristipomoides sieboldii* seemed to feed in a less regular temporal pattern with several peaks during the day and night. The highest catch rates of the *Etelis* species were widely separated in time; *E. coruscans* took bait most readily during 0600–0800 hours and *E. carbunculus* during 1800–2000 hours (Figure 2B). *Aprion virescens* was caught throughout the daylight hours, and seemingly was inactive during most of the night. The pooled CPUE for all snappers (which are targeted as a group in the snapper fishery) fluctuated over a diel cycle, with peaks during 0400–0800 hours and 1800–2200 hours. The pooled catch rate declined from 2200–0400 hours.

Distributions of CPUE at discrete depth intervals indicated that *A. virescens* took bait most readily in the shallowest zone occupied by these species (Figure 3B). Its distribution overlapped with that of *P. filamentosus*; however, the CPUE of the latter was highest in a deeper zone (100–150 m) (Figure 3A). The CPUE of *E. coruscans* was very low in all except our deepest (250–300 m) standardized fishing zone. The catch depth distributions of the two *Etelis* species overlapped, but the CPU for *E. carbunculus* was highest at 200–250 m depth and substantial at shallower depths. The catch depth distributions of the *Pristipomoides* species overlapped with that of *E. carbunculus*, but the peak CPUE of each species was in a different depth range. The peak CPUE for *P. sieboldii* was at 150–200 m. *Pristipomoides zonatus* was caught in the same depth range as *P. sieboldii*, but too few *P. zonatus* were caught to determine the depth where CPUE peaked. The depth range of some of these species may extend deeper than 300 m. However, local underwater observations (S. Ralston, personal communication) and research elsewhere in the tropical Pacific (Ralston and Williams 1988) suggest that none of the species has major peaks in abundance at depths exceeding 300 m.

Chi-square goodness-of-fit analysis indicated that within each depth and time interval sampled, catches (relative abundances) of these species varied significantly from an "expected" uniform distribution of equal catch of all species ($\chi^2$ = 11.73–521.04, df = 5, $P$ = 0.01–0.005). The nonuniform

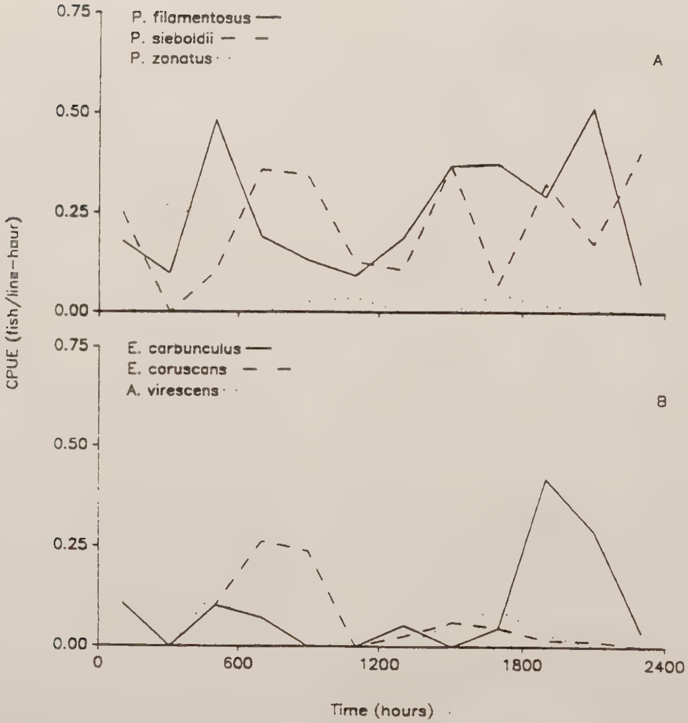

FIGURE 2.—Diel pattern of catch per unit effort (CPUE) of (A) three *Pristipomoides* species, and (B) two *Etelis* species and *Aprion virescens*, at Penguin Bank, Hawaii, 1987–1989.

dispersion of catches suggests that the differences in observed interspecific temporal and depth patterns of catch are related to real interspecific differences in patterns of predator occurrence and feeding.

To determine whether fish size was related to depth or time of capture, the catch data were tested by both median comparison tests and nonparametric correlation analysis. No significant correlation was found between fork length and capture depth for any of these species (Spearman's rank correlation analysis: $r_s = -0.13$–$0.29$, $P = 0.17$–$0.92$). For each of the species, median fork lengths of fish caught during daylight (0600–1830 hours) and darkness (1830–0600 hours) were not significantly different (Wilcoxon's signed-rank test: $Z = 0.98$–$1.61$, $P = 0.10$–$0.32$).

### *Fish Retrieval Rate and Regurgitation*

The effect of fish retrieval rate on regurgitation was tested for all species by Spearman's rank correlation analysis. No clearly significant correlation was found between rate of ascent and regurgitation index ($r_s = -0.23$–$0.01$, $P = 0.06$–$0.93$). However, qualitative observations indicated that a retrieval rate of about 0.5 m/s was optimal in terms of fish condition and fishing success. Fish retrieved rapidly (≥2 m/s) or very slowly (≤0.1 m/s) exhibited signs of traumatic decompression, including extreme eversion of the stomach through the esophagus, and bulging eyes. However, fish retrieved at intermediate rates of ascent (about 0.3–0.6 m/s) usually showed less traumatic signs of decompression and were often lively at the surface. Size of fish did not seem to affect the extent of regurgitation; the Spearman coefficients comparing fork length with regurgitation index were nonsignificant for all species ($r_s = 0.01$–$0.14$, $P = 0.72$–$0.94$). No significant correlation could be found between regurgitation index and the depth at which a fish was hooked (depth range, 49–280 m; $r_s = -0.007$–$0.27$, $P = 0.22$–$0.45$).

### *Trophic Analysis*

Analysis with diet overlap indices based on percent IRI indicated that for each species, the com-

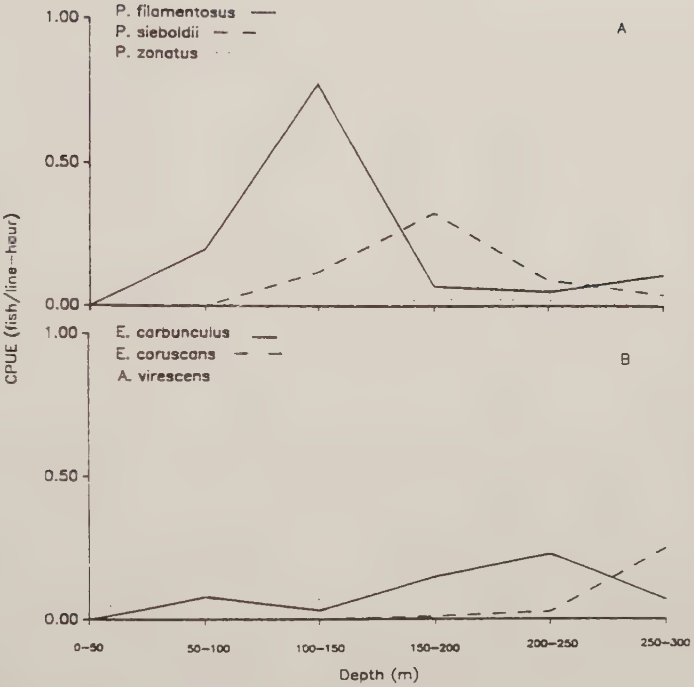

FIGURE 3.—Depth distributions of catch per unit effort (CPUE) of (A) three *Pristipomoides* species, and (B) two *Etelis* species and *Aprion virescens*, at Penguin Bank, Hawaii, 1987–1989.

position of prey items found in the hindgut, stomach, and mouth was similar ($C_\lambda$ > 0.5 for diet overlap between gut locations for each snapper species). Therefore, all prey items from the entire alimentary tract of an individual were pooled for diet calculations.

As a group, the snappers ate large amounts of a wide range of pelagic animals and much smaller quantities of a few benthic groups (Table 3; Appendix Table A.1). Five of the snapper species were separable by diet into two general feeding guilds: (1) zooplanktivores that fed primarily on pelagic urochordates, planktonic crustaceans, and pteropods, and (2) species that were primarily piscivorous (Table 3). Zooplankton composed 92% and 97% of the total IRI in the diets of *P. filamentosus* and *P. sieboldii*, respectively. *Etelis coruscans*, *E. carbunculus*, and *A. virescens* were primarily piscivorous; fish accounted for 81–98% of the total IRI.

*Pristipomoides* species fed on pelagic urochordates (mainly thaliaceans); these prey were most prevalent in the diet of *P. filamentosus* (47% of total IRI). *Pristipomoides sieboldii* also fed on thaliaceans (16% of total IRI), but pelagic crustaceans (47%) and pteropods (29%) were more important prey items. Pelagic crustaceans and pteropods were also important in the diet of *P. filamentosus*. *Pristipomoides zonatus* fed on thaliaceans (38% of total IRI), but also preyed on fish (55%) and benthic crustaceans (6%). In the piscivorous guild, pelagic urochordates, cephalopods, and benthic crustaceans also were notable prey items.

The two feeding guilds were clearly distinguished by their $C_\lambda$ values. Exclusive of *P. zonatus*, $C_\lambda$ values ranged from 0.78 to 1.00 within guilds (Table 4), and little dietary overlap occurred between guilds ($C_\lambda$ = 0.03–0.23). *Pristipomoides zonatus* (only six specimens) fell somewhat between guilds: it showed high overlap with the piscivorous guild ($C_\lambda$ = 0.76–0.87) and medium–low overlap with the zooplanktivorous guild ($C_\lambda$ = 0.18–0.55).

Major diel and seasonal diet changes were found only for *P. filamentosus*. Its $C_\lambda$ value (based on

TABLE 3.—Diets of six deepwater snapper species collected at Penguin Bank, Hawaii, in 1987–1989. Gut contents of 219 fish were divided into 12 major systematic or ecological groups. Relative abundance of prey is expressed as percentage of total index of relative importance (IRI). Numbers in parentheses indicate the number of guts with any identifiable contents.

| Prey group | Percent IRI in gut contents of | | | | | |
|---|---|---|---|---|---|---|
| | *Pristipomoides sieboldii* (60) | *Pristipomoides filamentosus* (54) | *Pristipomoides zonatus* (6) | *Etelis coruscans* (24) | *Etelis carbunculus* (33) | *Aprion virescens* (42) |
| Fish (juvenile and adult) | 1.8 | 7.2 | 55.2 | 80.6 | 98.4 | 95.8 |
| Fish larvae | 0.3 | 0.04 | 0.0 | 0.0 | 0.0 | 0.2 |
| Pelagic small crustaceans | 47.2 | 31.1 | 0.0 | 1.0 | 1.0 | 0.4 |
| Shrimp (adult)[a] | 1.2 | 0.1 | 0.7 | 4.4 | 0.2 | 0.1 |
| Crabs (adult)[a] | 0.07 | 0.0 | 5.8 | 0.06 | 0.03 | 0.02 |
| Polychaete worms | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Cephalopods | 1.5 | 0.5 | 0.0 | 2.9 | 0.3 | 0.7 |
| Pteropod molluscs | 28.9 | 13.0 | 0.0 | 0.0 | 0.0 | 0.01 |
| Other small molluscs | 0.4 | 0.2 | 0.0 | 0.0 | 0.02 | 0.0 |
| Chaetognaths | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Pelagic urochordates | 16.4 | 47.3 | 38.4 | 11.1 | 0.02 | 2.7 |
| Siphonophores | 1.8 | 0.6 | 0.0 | 0.0 | 0.0 | 0.0 |

[a] Larvae are included in "Pelagic small crustaceans."

IRI) for day versus night samples was 0.50. Pelagic urochordates composed a much greater part of the total IRI of individuals caught at night (Table 5). Other major components of the diet (e.g., fish, pelagic crustaceans) were more prevalent in specimens caught during the day. Seasonally, pelagic urochordates were low in the summer IRI of *P. filamentosus*, increased in winter, and became strongly dominant in spring (Table 5). As urochordates increased, groups such as pelagic crustaceans, pteropods and fish, which had composed sizable percentages of the IRI in summer or winter, decreased to low spring levels. Seasonal $C_\lambda$ values for *P. filamentosus* reflected the fluctuating importance of pelagic urochordates in the diet. Values of $C_\lambda$ for summer versus winter (0.78) and spring versus winter (0.71) were similar. However, the shift of the major diet component from pelagic crustaceans in summer to pelagic urochordates in spring resulted in a $C_\lambda$ value of 0.34 in the summer versus spring diet comparison. The diet of each piscivorous species was highly similar throughout the diel and seasonal cycles; the range of $C_\lambda$ values was 0.62–0.99.

## Discussion

### *Fish Retrieval Rate and Regurgitation*

Regurgitation of gut contents due to rapid decompression remains a problem for trophic studies of deepwater physoclistous fishes. We found that retrieval at a very slow rate to allow resorp-

TABLE 4.—Values of the index of diet overlap ($C_\lambda$) between each pairwise combination of six deepwater snapper species collected at Penguin Bank, Hawaii, in 1987–1989. Values of $C_\lambda$ are calculated based on percentage of index of relative importance (IRI).

| Species | *P. filamentosus* | *P. zonatus* | *E. coruscans* | *E. carbunculus* | *Aprion virescens* |
|---|---|---|---|---|---|
| *Pristipomoides sieboldii* | 0.78 | 0.18 | 0.08 | 0.03 | 0.04 |
| *Pristipomoides filamentosus* | | 0.55 | 0.23 | 0.11 | 0.13 |
| *Pristipomoides zonatus* | | | 0.87 | 0.76 | 0.78 |
| *Etelis coruscans* | | | | 0.97 | 0.98 |
| *Etelis carbunculus* | | | | | 1.00 |

TABLE 5.—Temporal trends in diet composition of *Pristipomoides filamentosus* at Penguin Bank, Hawaii, in 1987–1989. Gut contents were divided into eight major systematic or ecological groups. Relative abundance of prey is expressed as percentage of total index of relative importance (IRI). Numbers in parentheses indicate the number of guts in each period that contained any identifiable prey.

| | Percent IRI in gut contents collected during | | | | |
|---|---|---|---|---|---|
| Prey group | Day (35) | Night (19) | Summer (15) | Winter (25) | Spring (14) |
| Fish (juvenile and adult) | 10.0 | 1.7 | 13.6 | 9.4 | 1.6 |
| Fish larvae | 0.1 | <0.01 | 0.2 | 0.03 | <0.01 |
| Pelagic small crustaceans | 42.6 | 6.6 | 57.2 | 29.9 | 9.3 |
| Shrimp (adult)[a] | 0.1 | 0.1 | <0.01 | 0.02 | 0.7 |
| Cephalopods | 0.4 | 0.4 | 0.8 | 0.3 | 0.4 |
| Pteropod molluscs | 18.1 | 5.9 | 10.2 | 22.2 | 4.8 |
| Pelagic urochordates | 28.2 | 84.8 | 15.0 | 37.7 | 83.3 |
| Siphonophores | 0.5 | 0.7 | 2.9 | 0.4 | 0.03 |

[a] Larvae are included in "Pelagic small crustaceans."

tion of gases from the swim bladder is not a satisfactory solution. Fish retrieved at the slowest rates often showed the same signs of barotrauma as those retrieved rapidly. Their inactivity when landed and lack of the usual signs of life suggest that death or debilitation is common after a long period on the line. Such fish may have reduced physiological capability to resorb gas from the bladder (perhaps because of loss of nervous control of the oval; Harden Jones 1957). However, fish retrieved at an intermediate rate (about 0.5 m/s) appeared to be less severely affected and often contained intact stomachs or retained a substantial amount of prey in the mouth, gills, and gill rakers. Our results suggest that retrieving at moderate rates produces specimens usable for diet studies and is a practical procedure for a field sampling program.

Subsurface handling of individual fish by divers may be one way of reducing the problem of barotrauma in physoclistous fishes (Parrish and Moffitt 1993). However, this technique is not feasible with intensive fishing operations such as those used in the present study.

Our results suggest that the entire gastrointestinal tract should be examined to obtain the maximum diet information from a given sample. In this study, the diversity and composition of prey found in the intestines were sufficiently similar to those found in the stomach and mouth that prey from all parts of the alimentary tract could be pooled for dietary analysis. However, some of the soft-bodied prey (especially larval fishes) seemed to be underrepresented in the intestinal samples. Movement of food through the digestive tract of these fishes seems to be fairly rapid. "Palu" (a fish attractant composed of minced fish and oats) was found in the hindgut of three species (*A. virescens, P. filamentosus, E. coruscans*) caught 1–2.5 h after it was first released in the water.

### *Trophic Analysis*

Our data indicate that a distinct feeding guild with a strongly zooplanktonic diet occurs among the lutjanid snappers at Penguin Bank. These results, together with the reports for deepwater snappers elsewhere in the tropical Pacific (Parrish 1987), suggest that zooplanktivory may be an important trophic mode among *Pristipomoides* species. Examination of our data from all Penguin Bank cruises showed that zooplankton dominated the diets of *P. filamentosus* and *P. sieboldii* throughout the year, and levels of piscivory remained low. The diet composition of species of the piscivorous guild (*A. virescens, E. coruscans,* and *E. carbunculus*) remained relatively constant throughout the day and seasons of the year. *Pristipomoides zonatus* may have a more generalized diet than species in the planktivorous or piscivorous guilds. Our six specimens of *P. zonatus* contained substantial amounts of both benthic–demersal and pelagic forms. This same trend was reported for a larger sample ($N = 106$) of this species occurring in the Marianas (Seki and Callahan 1988).

As is commonly the case with analysis of fish gut contents, most of the fish prey we found in these deepwater snappers were not identifiable even to major groups. The identifiable fish prey were diverse systematically and ecologically, and included relatively sedentary species, fishes with generally demersal habits at a variety of depths, fishes of the water column near bottom, and mesopelagic species (Appendix). There was rather good correspondence between what is known of the common depth ranges of the various prey fishes and the depths at which the particular snapper species that ate them were collected.

The deep-feeding *Etelis* species contained a deepwater demersal cardinalfish *Epigonus* sp. and three identifiable mesopelagic fishes: the bristlemouth *Argyripnus brocki* and the lanternfishes *Benthosema fibulatum* and *Diaphus* sp. All these mesopelagic species have been identified as components of the distinctive "mesopelagic-boundary community" of Hawaii, which inhabits coastal waters over bottom depths of perhaps 100–700 m in a band surrounding islands and banks (Reid et al. 1991; S. B. Reid, University of Hawaii, personal communication). Of these species, at least *Benthosema fibulatum* and some *Diaphus* species perform some diel vertical migration and could be eaten well above the bottom at some times of the day. A number of the other, primarily demersal, prey species in the snapper diets also range higher in the water column at times and may be subject to midwater predation, especially during their younger life stages. The deepwater snappers may eat such prey only at the bottom, but these prey could provide a short link with productivity originating higher in the water column.

Monacanthidae (many identifiable as *Pervagor* sp.) were the most nearly ubiquitous prey fish, occurring in all the snapper species except one and composing at least a few percent of the diet of some. Species of *Pervagor*, especially the fantail filefish *P. spilosoma*, occasionally become extremely numerous and widely consumed by piscivorous fishes in Hawaii, at least in shallow waters (Tinker 1978; Brock 1984, 1985; Sudekum et al. 1991). At such times, this species seems to modify its usual behavior and occupies much of the water column as well as its usual demersal habitat (T. A. Clarke and S. B. Reid, University of Hawaii, personal communication). The abundance of monacanthids was not monitored at the specific times and locations of our collections. However, visual censuses made from submersibles on the top and upper slopes of Penguin Bank at 61–117 m depth between October 1985 and February 1988 (overlapping our study) showed that *P. spilosoma* was among the few most abundant fish species present on artificial reefs (F. A. Parrish, Honolulu Laboratory, National Marine Fisheries service, personal communication). The abundance of monacanthids in snapper diets may indicate opportunistic feeding during sporadic abundance of a particular prey.

Fishes recognizable as larval stages occurred with fairly high frequency in the guts of *P. sieboldii*, *P. filamentosus*, and *A. virescens*, but numbers and volumes eaten and the corresponding IRI values were rather low (Appendix). It seems likely that many larval fishes were among the unidentified fish remains or other unrecognizable gut material. The identified larval fish material was concentrated in the zooplanktivorous guild, but some was consumed by the shallowest feeding piscivore. This suggests that the larval fishes occurred and were captured along with invertebrate plankton.

For most of these snapper species, diet data from other sources are based on 1–60 specimens, except for 209 specimens of *P. zonatus* (Parrish 1987). These uneven data suggest that fish prey vary from fairly important to strongly dominant in the diets of these species in other localities. Results for *P. filamentosus* from the NWHI (Parrish 1987) indicated somewhat greater piscivory than at Penguin Bank. *Aprion virescens* and *E. carbunculus* in the NWHI were strongly piscivorous (as at Penguin Bank), and *P. zonatus* appeared more intermediate between piscivory and planktivory (Parrish 1987).

The diets of Penguin Bank snappers contained no identified prey fish species in common with snappers in the other Pacific localities reported. (In all the studies, relatively few prey fishes were identified to species.) Prey families shared by deepwater snappers at Penguin Bank and at other Indo-Pacific localities included Congridae, Apogonidae, Myctophidae, Synodontidae, Balistidae, and Ostraciidae, as well as unidentified tetraodontiform fishes (Parrish 1987).

Cephalopods (including octopus and squid) at Penguin Bank were eaten by all but one snapper species studied there, sometimes providing several percent of the diet (Appendix). The two *Etelis* species, which occurred deepest of all the snappers, contained deepwater ommastrephid and chiroteuthid squid. An early juvenile onychoteuthid species with somewhat shallower distribution was eaten by the shallower-feeding *P. sieboldii*. Cephalopods (including Ommastrephidae) have been found in the diets of all except two deepwater snapper species reported from elsewhere in the Pacific (Parrish 1987). They were fairly important in the diet of *P. filamentosus* in the NWHI.

Several groups of small malacostracans and the larvae of a few groups of large ones made up the bulk of the pelagic crustacean prey category in our study (Appendix). For some small crustaceans (e.g., amphipods, ostracods, isopods), it is not clear whether the habitat was pelagic, benthic, or both. However, these groups commonly occurred in fish guts with other clearly pelagic groups. Larval, juvenile, and adult lobsters, shrimp, and especially crabs and stomatopods were found in the diets of the snappers. Among identified stomatopod prey, species of *Squilla* and *Lysiosquilla* are moderately common as adults in shallow waters of Hawaii and may occur deeper as well. Adults of *Odontodactylus* spp. are unknown from shallow waters in Hawaii, but they have been trawled occasionally from deeper, soft bottoms (well below 100 m). Most of the large crustaceans in the diet were clearly benthic inhabitants as adults (e.g., the deepwater galatheid crab *Munida* sp.). Diet studies of deepwater snappers from other localities (Parrish 1987; Seki and Callahan 1988) have revealed amphipods, euphausids, isopods, crab and stomatopod larvae, and adult benthic crabs (including *Munida* sp. and other galatheids), stomatopods, shrimp, and lobsters.

Pelagic pteropods, including a major component from the family Cavolinidae, were eaten by three snapper species at Penguin Bank and were important prey for two species (Table 3, Appendix). Pteropods of the family Cavolinidae were a minor component of the diet of *P. zonatus* in the Marianas, fairly common in *P. multidens* in Western Samoa, and very abundant in *P. auricilla* in the Marianas (Parrish 1987; Seki and Callahan 1988).

The abundant pelagic urochordates, which were found in all the snapper species at Penguin Bank, included Salpida (probably a dominant group, but difficult to identify as remains), Doliolida, and Pyrosomida (Appendix). Pelagic urochordates (dominantly *Pyrosoma* sp.) have been identified in the diets of all except two deepwater snappers studied elsewhere in the Pacific (Parrish 1987). Siphonophores (dominantly Calycophora), a minor prey item for two snapper species at Penguin Bank (Appendix), have also been found in the diet of *P. auricilla* in the Marianas (Parrish 1987).

Pelagic urochordates and siphonophores might seem at first to offer little nutrition and to be unlikely preferred prey. Both are gelatinous, and the filter-feeding urochordates contain an indigestible cellulose tunic. However, both groups can concentrate large amounts of captured plankton prey in their guts (up to 20% of the body weight in some urochordates; Kashkina 1986), thus increasing their overall value as food. Both groups are colonial and form large interconnected aggregations of many individuals. They may enable snappers to forage with high efficiency. The frequency and abundance with which these soft-bodied megaplankton, together with the ciliary-feeding pteropods, appear in diets of most deepwater snappers sampled in the Pacific (Parrish 1987) suggest that they make a substantial contribution to the nutrition of demersal deepwater fish populations.

It is widely believed that these snapper species are strongly demersal (*A. virescens* less so than the others). This belief is based on behavior of related species, interpretation of sonar chromoscope images, much experience of commercial and recreational fishers, results of considerable experimental fishing, and underwater observations (including our own at Penguin Bank). The many strikes at our hooks near the bottom (none during the short time of lowering and retrieving the line) indicate that species with the full range of diets were in an active feeding state at the bottom during much of the day and night.

Animals from all the major pelagic prey categories consumed (Table 3) have been reported at times in substantial quantities at depths where these snappers were collected. In many cases, these prey were reported to be near bottom (Struhsaker 1973; Wiebe et al. 1979; Kashkina 1986; Grassle and Morse-Porteous 1987; Bathmann 1988; Childress et al. 1989; Reid et al. 1991; L. P. Madin, Woods Hole Oceanographic Institution, personal communication). These reports (some from Hawaii) are consistent with a pattern of near-bottom feeding by snappers. However, all available evidence does not exclude the possibility that significant feeding occurs far above the bottom.

Regardless of the level in the water column where feeding occurs, it is clear that planktonic animals provide an important conduit for transferring production from lower trophic levels in the water column to some large snapper species. These snappers occupy a demersal habitat that does not seem to be highly productive. The planktonic subsidy from the water column, facilitated by vertical migration of the zooplankton, may be important in maintaining fishable stocks of these deepwater snappers.

### Spatial and Temporal Distribution

A baited hook does not represent a natural prey item for these snappers, but for the purpose of this study, an increase in CPUE was assumed to represent an increase in feeding activity. Diel cycles in feeding activity appear to be common and somewhat species-specific among the lutjanid snappers on Penguin Bank. Peak feeding of all these snappers as a group occurred during the morning and evening.

Nakamura (1967) and Shomura and Nakamura (1969), sampling with nets at depths of 60–200 m around the Hawaiian island of Oahu, reported marked increases in the abundance of zooplankton during early morning and evening. They observed strong diel fluctuations in abundance of ostracods, euphausids, pteropods, and larval fish, all of which are prey species for the zooplanktivorous snappers. Many zooplanktonic species migrate to surface waters at night to feed and return to deeper water during the day (Levinton 1982). This vertical migration could increase the availability of these prey to deepwater snappers during dawn and dusk as the zooplankton migrate past snappers occupying steep slopes or sites of high bottom relief.

The apparent diel distribution of zooplankton in the water column and the increased feeding activity by *Pristipomoides* species during early morning and evening suggest that these snappers are opportunistic zooplanktivores. However, pelagic urochordates, which were important in the diets of these snappers in our study, were less abundant than some of the other vertically migrating zooplanktonic groups in the net collections of Nakamura (1967) and Shomura and Nakamura (1969).

In general, the diets of the planktivorous *Pristipomoides* species had a higher percentage of thaliaceans at night and more pelagic crustaceans and fish during the day. This trend may reflect the difference in visibility of these prey and the role of vision in their capture. Small crustaceans and fishes would be more visible during the day, while the nearly transparent thaliaceans would be hard to see. At night, the relatively low visual acuity of the fish eye would result in much reduced ability to resolve smaller prey targets (Hobson 1991; McFarland 1991). However, many thaliaceans are bioluminescent, which along with their colonial habit could make them much more visible than small crustaceans or fishes. Their slow locomotion and bulky colonial form may make them more vulnerable to capture by random encounter in the dark.

Shomura and Nakamura (1969) reported that abundance of thaliaceans in Hawaiian waters was relatively low in summer and fall, higher in winter, and highest in spring. We found a similar trend in the abundance of thaliaceans in the diet of *P. filamentosus* on Penguin Bank. Kashkina (1986) reviewed a number of studies that reported high abundance of thaliaceans in portions of the "Hawaiian range" and elsewhere where there was upward mixing of nutrient-rich waters in spring. He suggested that such conditions stimulated planktonic production and provided food for increased thaliacean populations.

### *Resource Partitioning*

Some of the snapper species caught in our study exhibited considerable overlap in diel feeding schedules. However, niche overlap was probably minimized by partitioning of prey and peak feeding depth. Within the piscivorous guild, dietary overlap was high. However, these species seemed to be stratified by bottom depth of peak feeding activity (Figure 3B). Little niche dimension overlap was evident between *A. virescens* and the other members of the piscivorous guild (or other snappers), because *A. virescens* fed most actively during daylight and much higher in the water column than the other species. Potential overlap seems most likely between *E. carbunculus* and *P. zonatus*, as all three niche dimensions measured showed considerable overlap. However, we collected too few *P. zonatus* to permit estimating the degree of overlap with confidence. For the two strongly zooplanktivorous *Pristipomoides* species, both diets and diel feeding schedules overlapped considerably. However, peak feeding activity seemed to occur at a bottom depth about 50 m deeper for *P. sieboldii* than for *P. filamentosus*. Moderate overlap in all three measured niche dimensions seemed to occur between *P. filamentosus* and *P. zonatus*, but interpretation was difficult because of the small sample size of *P. zonatus*. Based on diet composition and depth and time of catch, strong niche overlap between the planktivorous and piscivorous guilds seems unlikely.

### *Fishery Implications*

Recent studies indicate that *P. filamentosus*, *E. coruscans*, and *E. carbunculus* have suffered significant growth overfishing around the main (inhabited) Hawaiian Islands and that *A. virescens* may have suffered some such effects (Ralston and Kawamoto 1988; Somerton and Kobayashi 1990a). Major reductions in spawning stock biomass of the first two species are raising concern among fisheries managers that they also may be experiencing recruitment overfishing (WPRFMC 1991).

Imposing size limits for retention of snappers has been suggested as a way to reduce the mortality of immature fish, increase the yield per recruit, and protect against recruitment overfishing (Somerton and Kobayashi 1990b). However, capture and release seems to result in high mortality, and the full benefits of a minimum size limit would be realized only if catches of undersize fish were minimized. This would be possible if undersize fish were naturally segregated from the larger fish by capture depth or time. However, the results presented here do not indicate that such stratification occurs. A possible approach to size-selective line fishing may be a judicious choice of hook size (Ralston 1990).

It seems unlikely that any foreseeable developments in gear or techniques will permit the fishery to harvest these stocks with high selectivity by species. However, our results are consistent with the reports of fishers that considerable selectivity can be achieved by choice of depth fished.

Population parameters and the ecology of individual species are often poorly known in tropical multispecies fisheries. Thus, groups of species such as deepwater snappers are sometimes analyzed and managed as a unit by approaches such as the total-biomass Schaefer model (TBSM) (Ralston and Polovina 1982). However, a thorough understanding of trophic relationships among the species making up the fishery is important for management of any multispecies fishery, and application of the TBSM may be inappropriate if such relationships remain unknown (May et al. 1979; Pauly 1979). The large differences in trophic roles of some of the snapper species at Penguin Bank suggest caution in lumping these species together in a TBSM analysis.

This study has not fully revealed the sources or production processes supporting these snapper populations. It is plausible that the productivity of the bank as a whole is enhanced by its hydrography. However, much of the food of these snapper species comes from pelagic (planktonic or nektonic) animals. This suggests that the occurrence and abundance of snappers on these grounds is not the result of some concentrated benthic food resource that is highly specific to localized bottom features. Bank features may provide some other localized resource (e.g., vertical relief, protective cover) that is important to snappers.

The distribution of these snappers may be affected by the upward deflection of deeper currents where the currents encounter the higher relief of banks, resulting in a higher local abundance of plankton (e.g., Brock and Chamberlain 1968). In an ecological study of the bottom fish resources of Johnston Atoll, Ralston et al. (1986) found *P. filamentosus* in much higher densities on the upcurrent side of the atoll than on the downcurrent side. They postulated that this was related to increased availability of allochthonous planktonic prey in the neritic upcurrent areas due to oceanic currents deflected by the atoll.

Although deepwater banks in Hawaii and the Pacific support highly productive fishery resources, their ecology remains relatively obscure. The results presented here are based on our collections from the south-central portion of Penguin Bank. These results provide a substantial contribution to knowledge of the trophic ecology of lutjanid snappers that support important deepwater fisheries on the bank and elsewhere throughout the Hawaiian Archipelago and other tropical seas.

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**Appendix follows**

## Appendix: Diets of Deepwater Snappers

TABLE A.1.—Diets of six deepwater snapper species collected at Penguin Bank, Hawaii, in 1987–1989. Shown are the percentages of predator individuals that consumed each prey (*F*), the percentages of all numbers (*N*) and volume (*V*) provided by each prey, and each prey's index of relative importance (IRI) in gut contents. The number of guts with any identifiable contents is indicated beside each snapper species in parentheses. Prey categories followed by an asterisk are also included in the larger ecological category "Pelagic small Crustacea." Values for the highest systematic levels are underlined. Values of IRI were calculated separately for each prey category (line entry); values may be compared across categories at comparable systematic levels.

| Prey category | Percent frequency (*F*) | Percent number (*N*) | Percent volume (*V*) | IRI |
|---|---|---|---|---|
| | | ***Pristipomoides sieboldii* (60)** | | |
| Fish (all)[a] | 21.7 | 1.4 | 22.8 | 527.4 |
| Fish (juvenile and adult) | 10.0 | 0.4 | 21.2 | 216.7 |
| Congridae | | | | |
| Tetraodontiformes (all) | 1.7 | 0.1 | 3.0 | 5.2 |
| Monacanthidae | 1.7 | 0.1 | 3.0 | 5.2 |
| *Pervagor* sp. | | | | |
| Ostraciidae | | | | |
| Fish unidentified | 8.3 | 0.4 | 18.2 | 154.8 |
| Fish larvae[a] | 15.0 | 1.0 | 1.6 | 40.0 |
| Pelagic small Crustacea[a]* (including shrimp and crab larvae) | 91.7 | 44.7 | 18.2 | 5,758.8 |
| Euphausiacea* | 38.3 | 14.0 | 1.0 | 577.3 |
| Copepoda* | 26.7 | 10.2 | 0.8 | 292.6 |
| Amphipoda* | 43.3 | 4.5 | 0.3 | 211.0 |
| Hyperiidea | 3.3 | 0.1 | 0.01 | 0.4 |
| Gammaroidea | 5.0 | 0.2 | 0.01 | 1.0 |
| Caprellidea | 1.7 | 0.06 | <0.01 | 0.1 |
| Amphipoda unidentified | 38.3 | 4.2 | 0.3 | 171.7 |
| Isopoda* | 18.3 | 1.8 | 0.1 | 34.5 |
| Shrimp (all) | 38.3 | 5.1 | 8.3 | 511.6 |
| Shrimp (adult)[a] | 35.0 | 4.0 | 0.3 | 150.0 |
| Pandalidae | | | | |
| Shrimp unidentified | 35.0 | 4.0 | 0.3 | 150.0 |
| Shrimp larvae* | 1.7 | 0.1 | 0.01 | 0.2 |
| Alpheidae larvae | 1.7 | 0.06 | <0.01 | 0.1 |
| Zoea unidentified | 10.0 | 1.0 | 8.0 | 89.3 |
| Crabs (all) | 30.0 | 1.9 | 1.6 | 106.7 |
| *Munida* sp. (Galatheidae) | | | | |
| Crabs (adult, unidentified)[a] | 5.0 | 0.2 | 1.5 | 8.4 |
| Crab larvae (megalopa)* | 28.3 | 1.8 | 0.1 | 53.3 |
| Lobster (Palinuridae) larvae* | 1.7 | 0.06 | <0.01 | 0.1 |
| Stomatopoda larvae* | 26.7 | 1.9 | 7.1 | 240.9 |
| *Squilla* spp. larvae | 11.7 | 0.6 | 1.0 | 18.3 |
| *Lysiosquilla* spp. larvae | 6.7 | 0.6 | 5.0 | 37.2 |
| *Odontodactylus* spp. larvae | | | | |
| Stomatopoda larvae unidentified | 10.0 | 0.7 | 1.2 | 18.8 |
| Mysidacea* | 15.0 | 1.5 | 0.1 | 23.4 |
| Ostracoda* | 30.0 | 5.6 | 0.4 | 181.1 |
| Crustacea unidentified* | 30.0 | 2.3 | 0.2 | 74.0 |
| Polychaeta[a] | 13.3 | 1.2 | 0.1 | 17.3 |
| Cephalopoda[a] | 11.7 | 0.5 | 15.5 | 186.5 |
| Squid (all) | 3.3 | 0.1 | 0.3 | 1.5 |
| *Onychoteuthis* sp. | 1.7 | 0.06 | 0.3 | 0.6 |
| Squid unidentified | 1.7 | 0.06 | <0.01 | 0.1 |
| Octopoda unidentified | 1.7 | 0.06 | <0.01 | 0.1 |
| Cephalopoda unidentified | 6.7 | 0.3 | 15.2 | 103.2 |
| Pteropoda (all)[a] | 93.3 | 35.2 | 2.6 | 3,532.3 |
| *Cavolinia* spp. | 60.0 | 9.0 | 0.7 | 580.3 |
| *Clio* spp. | 46.7 | 7.6 | 0.6 | 381.7 |
| *Cuvierina* spp. | 58.3 | 8.1 | 0.6 | 507.4 |
| *Diacra* spp. | 46.7 | 5.5 | 0.4 | 275.7 |
| Pteropoda unidentified | 33.3 | 5.0 | 0.4 | 179.6 |
| Other small molluscs[a] | 26.7 | 1.8 | 0.1 | 51.9 |
| *Cymatium*/*Bursa* | 1.7 | 0.06 | <0.01 | 0.1 |
| Mollusca unidentified | | | | |
| Micromolluscs unidentified | 25.0 | 1.8 | 0.1 | 47.1 |

TABLE A.1.—Extended.

| Percent frequency (*F*) | Percent number (*N*) | Percent volume (*V*) | IRI | Percent frequency (*F*) | Percent number (*N*) | Percent volume (*V*) | IRI |
|---|---|---|---|---|---|---|---|
| ***Pristipomoides filamentosus* (54)** | | | | ***Pristipomoides zonatus* (6)** | | | |
| 20.4 | 3.2 | 33.8 | 752.2 | 66.7 | 33.3 | 76.9 | 7,346.8 |
| 18.5 | 2.5 | 33.5 | 665.2 | 66.7 | 33.3 | 76.9 | 7,346.8 |
| | | | | 16.7 | 5.6 | 12.8 | 306.1 |
| 3.7 | 0.4 | 4.8 | 19.0 | 16.7 | 5.6 | 12.8 | 306.1 |
| 1.9 | 0.2 | 2.4 | 4.8 | 16.7 | 5.6 | 12.8 | 306.1 |
| | | | | 16.7 | 5.6 | 12.8 | 306.1 |
| 1.9 | 0.2 | 2.4 | 4.8 | | | | |
| 16.7 | 2.1 | 28.8 | 515.0 | 50.0 | 22.2 | 51.2 | 3,673.4 |
| 3.7 | 0.7 | 0.3 | 3.7 | | | | |
| 46.3 | 49.1 | 12.6 | 2,859.9 | | | | |
| | | | | | | | |
| 7.4 | 2.1 | 0.04 | 15.9 | | | | |
| 7.4 | 1.2 | 0.02 | 9.3 | | | | |
| 1.9 | 0.2 | <0.01 | 0.3 | | | | |
| | | | | | | | |
| 1.9 | 0.2 | <0.01 | 0.3 | | | | |
| 9.3 | 1.2 | 0.02 | 11.6 | | | | |
| 9.3 | 1.2 | 2.0 | 29.6 | 16.7 | 5.6 | 0.02 | 92.9 |
| 7.4 | 0.7 | 0.8 | 11.1 | | | | |
| 1.9 | 0.2 | 0.4 | 1.0 | | | | |
| 5.6 | 0.5 | 0.4 | 5.1 | | | | |
| | | | | | | | |
| 3.7 | 0.5 | 1.2 | 6.3 | | | | |
| 14.8 | 6.3 | 0.1 | 95.5 | 33.3 | 16.7 | 6.3 | 765.7 |
| | | | | 16.7 | 5.6 | 2.1 | 127.6 |
| | | | | 16.7 | 11.1 | 4.2 | 255.2 |
| 14.8 | 6.3 | 0.1 | 95.5 | | | | |
| | | | | | | | |
| 9.3 | 21.6 | 10.9 | 301.0 | | | | |
| 5.6 | 19.5 | 8.5 | 155.2 | | | | |
| 5.6 | 0.7 | 1.6 | 12.6 | | | | |
| 1.9 | 0.2 | 0.4 | 1.0 | | | | |
| 5.6 | 1.2 | 0.5 | 9.8 | | | | |
| 3.7 | 1.4 | 0.03 | 5.3 | | | | |
| 11.1 | 11.1 | 0.2 | 125.3 | | | | |
| 22.2 | 3.5 | 0.07 | 79.6 | | | | |
| | | | | | | | |
| 5.6 | 0.5 | 7.2 | 42.9 | | | | |
| | | | | | | | |
| 5.6 | 0.5 | 7.2 | 42.9 | | | | |
| 55.6 | 21.1 | 0.4 | 1,193.2 | | | | |
| 22.2 | 4.9 | 0.1 | 111.4 | | | | |
| 22.2 | 6.3 | 0.1 | 143.2 | | | | |
| 13.0 | 2.1 | 0.04 | 27.8 | | | | |
| 25.9 | 6.5 | 0.1 | 171.7 | | | | |
| 9.3 | 1.2 | 0.02 | 11.6 | | | | |
| 9.3 | 2.1 | 0.04 | 19.9 | | | | |
| | | | | | | | |
| 1.9 | 0.2 | <0.01 | 0.3 | | | | |
| 7.4 | 1.9 | 0.04 | 14.6 | | | | |

TABLE A.1.—Continued.

| Prey category | Percent frequency (*F*) | Percent number (*N*) | Percent volume (*V*) | IRI |
|---|---|---|---|---|
| | | ***Pristipomoides sieboldii*** **(60)** | | |
| Chaetognatha[a] | 13.3 | 1.1 | 0.09 | 16.4 |
| Pelagic urochordates[a] | 46.7 | 4.7 | 38.3 | 2,006.0 |
| Thaliacea | 38.3 | 4.2 | 34.3 | 1,476.6 |
| *Pyrosoma* sp. | 8.3 | 0.4 | 3.0 | 27.9 |
| *Doliolum* sp. | 1.7 | 0.1 | 1.0 | 1.9 |
| Siphonophora[a] | 40.0 | 5.2 | 0.4 | 223.3 |
| Diphyidae | 40.0 | 5.1 | 0.4 | 218.1 |
| Abylidae (calycophoran) | 1.7 | 0.1 | 0.01 | 0.2 |
| Siphonophora unidentified | | | | |
| | | ***Etelis coruscans*** **(24)** | | |
| Fish (all)[a] | 62.5 | 30.4 | 85.7 | 7,253.4 |
| Fish (juvenile and adult) | 62.5 | 30.4 | 85.7 | 7,253.4 |
| *Argyripnus brocki* | | | | |
| *Benthosema fibulatum* | | | | |
| *Diaphus* sp. (*adenomus*?) | 4.2 | 0.9 | 0.03 | 3.8 |
| *Epigonus* sp. | 4.2 | 0.9 | 0.1 | 4.2 |
| Sphyraenidae | | | | |
| *Parupeneus* sp. (Mullidae) | | | | |
| *Naso* sp. (Acanthuridae) | | | | |
| *Naso hexacanthus* | | | | |
| *Dactyloptena orientalis* | | | | |
| *Pegasus papilio* | | | | |
| Tetraodontiformes (all) | | | | |
| Balistidae | | | | |
| Monacanthidae | | | | |
| *Pervagor* sp. | | | | |
| Monacanthidae unidentified | | | | |
| Tetraodontiform unidentified | | | | |
| *Antennarius pictus* | | | | |
| Fish unidentified | 54.2 | 28.6 | 71.3 | 5,411.3 |
| Fish larvae[a] | | | | |
| Synodontidae larvae | | | | |
| Fish larvae unidentified | | | | |
| Pelagic small Crustacea[a]* | 16.7 | 5.4 | 0.02 | 89.7 |
| Copepoda* | | | | |
| Isopoda* | | | | |
| Shrimp (all)[a] | 29.2 | 13.4 | 0.06 | 392.4 |
| *Heterocarpus ensifer* | 4.2 | 2.7 | 0.01 | 11.2 |
| Shrimp unidentified | 25.0 | 10.7 | 0.04 | 268.8 |
| Crabs (all)[a] | 4.2 | 0.9 | 0.4 | 5.6 |
| Hippoidea | 4.2 | 0.9 | 0.4 | 5.2 |
| Crabs (adult, unidentified) | | | | |
| Crab larvae (megalopa)* | | | | |
| Stomatopoda (adult) | | | | |
| *Odontodactylus hanseni* | | | | |
| Crustacea unidentified* | 16.7 | 5.4 | 0.02 | 89.6 |
| Cephalopoda[a] | 16.7 | 4.5 | 11.3 | 263.3 |
| Squid (all) | 4.2 | 1.8 | 3.3 | 21.2 |
| *Chiroteuthis* sp. | | | | |
| *Nototodarus hawaiiensis* | 4.2 | 1.8 | 2.8 | 19.0 |
| Squid unidentified | | | | |
| Octopoda unidentified | | | | |
| Cephalopoda unidentified | 12.5 | 2.7 | 6.7 | 117.1 |
| Pteropoda[a] | | | | |
| *Diacra* sp. | | | | |
| Other small molluscs[a] | | | | |
| Pelagic urochordates[a] | 20.8 | 45.5 | 2.4 | 999.7 |
| Thaliacea | 20.8 | 45.5 | 2.4 | 999.7 |
| Salpidae | | | | |
| *Pyrosoma* sp. | 20.8 | 45.5 | 2.4 | 999.7 |

[a] A major systematic or ecological group in Table 3.

TABLE A.1.—Extended. Continued.

| Percent frequency (*F*) | Percent number (*N*) | Percent volume (*V*) | IRI | Percent frequency (*F*) | Percent number (*N*) | Percent volume (*V*) | IRI |
|---|---|---|---|---|---|---|---|
| ***Pristipomoides filamentosus* (54)** | | | | ***Pristipomoides zonatus* (6)** | | | |
| 66.7 | 20.2 | 45.1 | 4,350.7 | 83.3 | 44.4 | 16.8 | 5,104.4 |
| 50.0 | 16.3 | 36.6 | 2,645.9 | 83.3 | 44.4 | 16.8 | 5,104.4 |
| 22.2 | 3.9 | 8.7 | 278.2 | | | | |
| | | | | | | | |
| 18.5 | 3.2 | 0.06 | 59.7 | | | | |
| 14.8 | 2.1 | 0.04 | 31.8 | | | | |
| | | | | | | | |
| 3.7 | 1.1 | 0.02 | 4.0 | | | | |
| ***Etelis carbunculus* (33)** | | | | ***Aprion virescens* (42)** | | | |
| 90.9 | 78.9 | 95.7 | 15,871.3 | 92.9 | 67.6 | 91.6 | 14,783.1 |
| 90.9 | 78.9 | 95.7 | 15,871.3 | 88.1 | 64.1 | 91.5 | 13,704.8 |
| 3.0 | 2.2 | 0.2 | 7.2 | | | | |
| 3.0 | 2.2 | 0.02 | 6.8 | | | | |
| | | | | | | | |
| | | | | | | | |
| | | | | 2.4 | 0.7 | 0.03 | 1.8 |
| | | | | 2.4 | 1.4 | 0.2 | 3.9 |
| | | | | 11.9 | 4.9 | 0.3 | 61.7 |
| | | | | 2.4 | 0.7 | 0.5 | 3.0 |
| | | | | 2.4 | 0.7 | 0.03 | 1.8 |
| | | | | 2.4 | 0.7 | 0.1 | 2.0 |
| 15.2 | 32.2 | 41.3 | 1,114.6 | 9.5 | 5.6 | 5.2 | 102.9 |
| | | | | 2.4 | 0.7 | 0.1 | 1.8 |
| 15.2 | 32.2 | 41.3 | 1,114.6 | 4.8 | 2.8 | 4.8 | 36.6 |
| 12.1 | 22.2 | 28.5 | 615.0 | | | | |
| 6.1 | 10.0 | 12.8 | 138.4 | | | | |
| | | | | 4.8 | 2.1 | 0.2 | 11.1 |
| | | | | 2.4 | 0.7 | 1.0 | 4.0 |
| 81.8 | 42.2 | 54.2 | 7,886.7 | 78.6 | 48.6 | 84.1 | 10,426.4 |
| | | | | 9.5 | 3.5 | 0.1 | 34.6 |
| | | | | 4.8 | 2.1 | 0.04 | 10.2 |
| | | | | 4.8 | 1.4 | 0.08 | 7.1 |
| 18.2 | 7.8 | 1.4 | 167.0 | 14.3 | 4.2 | 0.01 | 60.5 |
| 3.0 | 1.1 | <0.01 | 3.4 | | | | |
| | | | | 2.4 | 0.7 | <0.01 | 1.7 |
| 9.1 | 3.3 | 0.7 | 36.7 | 7.1 | 2.8 | <0.01 | 20.2 |
| | | | | | | | |
| 9.1 | 3.3 | 0.7 | 36.7 | | | | |
| 3.0 | 1.1 | 0.2 | 4.1 | 7.1 | 2.1 | 0.2 | 16.5 |
| | | | | | | | |
| 3.0 | 1.1 | 0.2 | 4.1 | 2.4 | 0.7 | 0.2 | 2.2 |
| | | | | 4.8 | 1.4 | <0.01 | 6.7 |
| | | | | 2.4 | 0.7 | 0.08 | 1.9 |
| | | | | 2.4 | 0.7 | 0.08 | 1.9 |
| 18.2 | 6.7 | 1.4 | 146.7 | 7.1 | 2.1 | <0.01 | 15.1 |
| 6.1 | 6.7 | 1.7 | 50.9 | 11.9 | 3.5 | 4.9 | 100.0 |
| 6.1 | 6.7 | 1.7 | 50.9 | | | | |
| 3.0 | 2.2 | 0.3 | 7.6 | | | | |
| 3.0 | 1.1 | 1.4 | 7.7 | | | | |
| 3.0 | 3.3 | 0.01 | 10.1 | | | | |
| | | | | 2.4 | 0.7 | <0.01 | 1.7 |
| | | | | 9.5 | 2.8 | 4.9 | 73.3 |
| | | | | 2.4 | 0.7 | <0.01 | 1.7 |
| | | | | 2.4 | 0.7 | <0.01 | 1.7 |
| 3.0 | 1.1 | <0.01 | 3.4 | | | | |
| 3.0 | 1.1 | 0.2 | 4.1 | 16.7 | 19.7 | 3.2 | 382.3 |
| 3.0 | 1.1 | 0.2 | 4.1 | 14.3 | 11.3 | 3.2 | 206.7 |
| | | | | 2.4 | 8.5 | 0.02 | 20.2 |

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# The Western Pacific Fishery Information Network: A Fisheries Information System

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*ABSTRACT—The Western Pacific Fishery Information Network (WPACFIN) is an intergovernmental agency cooperative program sponsored by the National Marine Fisheries Service (NMFS) to help participating island fisheries agencies carry out data collection, analysis, reporting programs, and data management activities to better support fisheries management under the Magnuson Fishery Conservation and Management Act; and to help meet local fisheries information and management needs. The WPACFIN is the central source of information for Federal fisheries management of most fisheries in American Samoa, Guam, and the Northern Mariana Islands, and it plays an important role in acquiring fisheries data in Hawaii. This paper describes the development and status of this fishery information system.*

### Introduction

Fisheries in the Pacific have been rapidly changing during the 1980's, and fisheries agencies have been changing with them to obtain and utilize the proper data and information needed to monitor and manage the resources under their jurisdictions. To help meet the ever growing and changing information needs of fishery agencies of the Pacific, the National Marine Fisheries Service (NMFS) established a Pacific Fishery Information Network (PACFIN) for the western coastal states and Idaho, and the Western Pacific Fishery Information Network (WPACFIN) for the U.S.-affiliated fishery agencies in the central and western Pacific island areas of American Samoa, Hawaii, Guam, and the Northern Mariana Islands. This paper is exclusively concerned with WPACFIN.

Through the NMFS WPACFIN program, an organization of cooperating island fisheries agencies has developed a network to share data, information, and technology to improve fisheries management under the Magnuson Fishery Conservation and Management Act and to meet local fisheries management needs. The voluntary and cooperative nature of the network cannot be overemphasized, for these attributes are the backbone of the existence of the system. The information available through WPACFIN has been developed through cooperative efforts of the participating agencies to improve their data collection, compilation, computerization, and summarization capabilities by means of technical assistance provided by the central WPACFIN program at the Honolulu Laboratory and by means of financial assistance from various NMFS and other funding sources.

From the beginning, it has been the philosophy and policy of the WPACFIN program to adopt the general NMFS policy of building upon local fisheries office expertise and capabilities as a means of improving Federal fishery management capabilities. The WPACFIN system embodies the general principles of a Federal and state partnership and a symbiotic relationship in collecting, processing, analyzing, sharing, and managing fisheries data, and builds upon the history of cooperation among agencies. From the standpoint of the NMFS, the overall functional goal of the WPACFIN system is to provide quality fisheries data needed to develop, implement, evaluate, and amend Federal fishery management plans (FMP's) for the western Pacific region. The information needed to manage Federal fisheries under MFCMA should be a composite subset of information required by fully functional local fisheries agencies. Therefore, the operating philosophy of the central WPACFIN office in working with island agencies has been to assist them in becoming fully functional in obtaining and providing data and information needed to meet both Federal and local fishery management needs. By building upon the capabilities of local agencies, efficiency, benefits, functionality, and data availability can be maximized while overall costs and duplication of effort can be minimized. Accomplishing this requires significant levels of commitment on both sides and a common goal for improved fisheries management.

### The WPACFIN system

The use of the term WPACFIN is sometimes confusing because it can be used to refer to any of the three distinct but interrelated major aspects of the system that are embodied in the concept of a cooperative fishery information network, or it can refer to the "system" as a whole. The three aspects of the WPACFIN system are its 1) organization, 2) program, and 3) network. These are all intertwined and inseparable as far as the functionality of the WPACFIN system is concerned.

The WPACFIN organization refers to the combination of participating agencies and how they interact to make decisions and recommendations for improving fishery management capabilities in the region. The participating agencies of WPACFIN (Fig. 1) include the Western Pacific Regional Fishery Management Council (WPRFMC or Council), the American Samoa Department of Marine and Wildlife Resources (DMWR), the Commonwealth of the Northern Mariana Islands' Division of Fish and Wildlife (DFW), the Guam Division of Aquatic and Wildlife Resources (DAWR) and Department of Commerce (DOC), the Hawaii Division of Aquatic Resources (HDAR), and the Honolulu Laboratory and Pacific Area Office of the NMFS. For simplicity, this paper will refer to the island fisheries offices not based in Hawaii as the "flag state" agencies.

To help coordinate all the participating agencies and to help set goals and priorities for meeting the information needs through WPACFIN, a committee composed of all the heads of the participating fisheries agencies was established in 1982. This committee was originally named the WPACFIN Data Goals Committee, but was later renamed the WPACFIN Fisheries Data Coordinating Committee (FDCC). The FDCC is the advisory body within the WPACFIN organization. The intent of the committee is to ensure that all required data are available to each participating agency and to the Western Pacific Regional Fishery Management Council, its Plan Monitoring Teams, its Scientific and Statistical Committee, and fishery managers, in a form, quality, and time frame necessary to meet their respective fisheries management responsibilities. Specifically stated, the purposes of the WPACFIN FDCC are to:

1) Provide a forum for a regional exchange of ideas about fisheries data and for meeting local and regional fishery management goals;

2) Establish WPACFIN activities and priorities and recommend improvements in efficiency, effectiveness, and timeliness of data collecting and processing activities;

3) Develop and coordinate a WPACFIN Fisheries Data Plan for implementation in each member area;

4) Promote the development and implementation of data collection, storage, and transfer standards to facilitate merging data into WPACFIN; and

5) Designate membership of a Technical Subcommittee and coordinate the Subcommittee's work on technical aspects of implementing WPACFIN.

The FDCC also established guidelines for the proper exchange and use

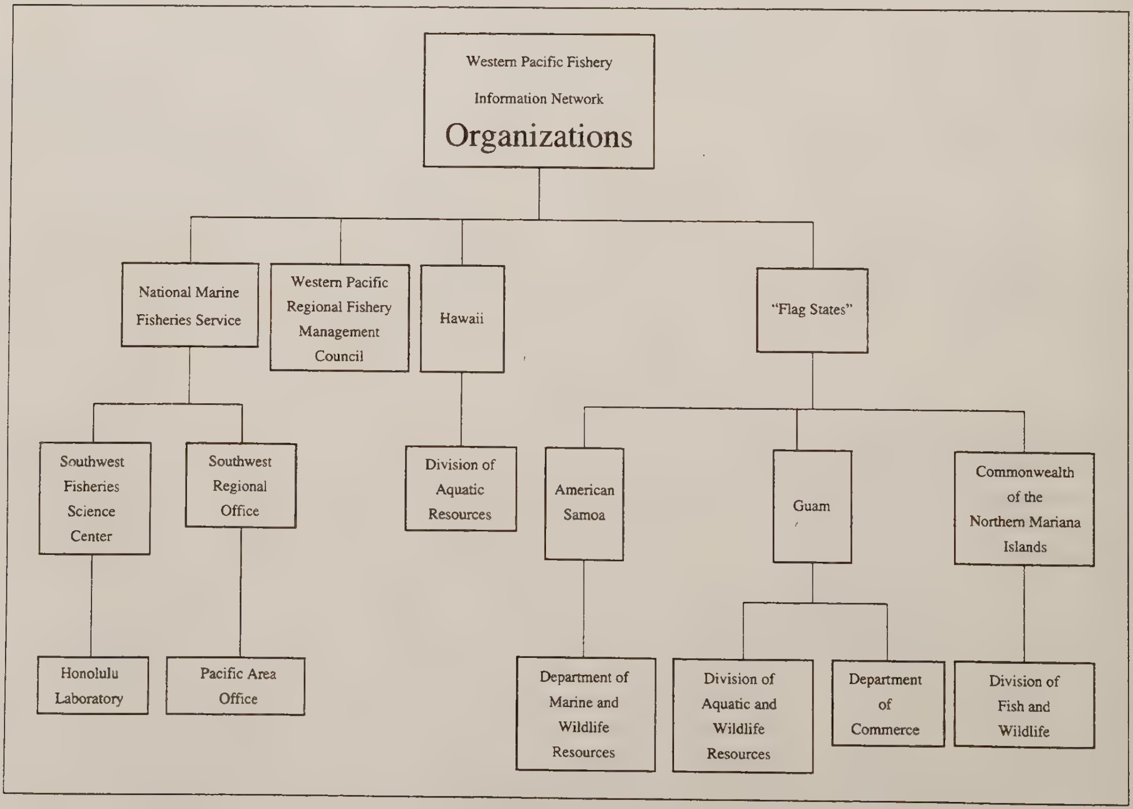
Western Pacific Fishery
Information Network
Organizations
National Marine Fisheries Service
Western Pacific Regional Fishery Management Council
Hawaii
"Flag States"
Southwest Fisheries Science Center
Southwest Regional Office
Division of Aquatic Resources
American Samoa
Guam
Commonwealth of the Northern Mariana Islands
Honolulu Laboratory
Pacific Area Office
Department of Marine and Wildlife Resources
Division of Aquatic and Wildlife Resources
Department of Commerce
Division of Fish and Wildlife

Figure 1.—Organizations participating in the Western Pacific Fishery Information Network.

of fishery data and for safeguarding the confidentiality of data submitted by member agencies:

1) WPACFIN will not release confidential data in any format without specific written permission from the agency contributing the data to the system.

2) Requests for raw (nonsummary) data or requests from nonmember agencies will be referred to the donor agency.

3) If access is granted by the donor agency, WPACFIN may provide the data directly to the user from the central system at the donor agency's request.

4) Confidential data submitted to WPACFIN are generally available for NMFS employees to use provided the employee has signed a Statement of Nondisclosure and has a "need-to-know" as defined in NOAA Directive 88–30.

5) Summary and nonconfidential data in WPACFIN are available to all users without obtaining donor agency approval.

6) Specific restrictions may be placed on sensitive data sets submitted to WPACFIN that could limit access to users identified by the donor agency.

The WPACFIN program is a task within the Fishery Data Management Program of the NMFS Honolulu Laboratory's Fishery Management and Performance Investigation. It was established in 1981 to be the nucleus for organizing, implementing, and maintaining the fisheries information network in the western Pacific. The WPACFIN program is headed by the leader of the Fishery Data Management Program, and its staff has expertise in computer systems design, fisheries biology, and computer programming. The types of support offered by the WPACFIN program cover a variety of administrative and technical activities. Because of differences in data collecting and processing systems, political atmosphere, personnel, and level of commitment to upgrade and change, the flag state agencies have been the major focus of implementing the WPACFIN system, and they have been the major users of support offered by the WPACFIN program. Description of some of the major WPACFIN program support activities follows.

1) Administrative support has been provided at all levels for overseeing the WPACFIN program management, budgeting, and planning activities, such as developing and implementing "memoranda of understanding" and data sharing agreements between NMFS and participating agencies, and coordinating meetings of the FDCC and its Technical Subcommittee.

2) Technical hardware and software support has been crucial to developing local expertise.

3) System and survey designs have been studied in all areas, either by using consultant contracts or in-house NMFS expertise and resources (CIC Research, Inc.[1, 2], Omnitrak Research and Marketing Group, Inc.[3], and Malvestuto[4]).

4) Data base management and data processing systems have been established for many data systems such as commercial landings, offshore and inshore creel surveys, tuna transshipment, tournament sampling, vessel inventory, and fishery imports. Integrated, menu-driven, user-friendly, data base management systems have been developed and programmed to meet the needs of island agencies.

5) A wide range of training support has been provided to island agencies including on-site and central training workshops on microcomputer hardware and software, data base and file management, data quality control procedures, data collecting, forms design, and detailed training on implementing the data processing applications.

6) Fisheries data bases provided to the system by participating agencies are maintained at the central WPACFIN program office. Direct online access to some of these centralized data bases is a long-range goal.

7) Numerous report generation and data analysis activities, such as filling ad-hoc data requests, assisting in producing the flag state agencies' report modules for the annual bottomfish and pelagics plan monitoring teams (Hamm and Quach[5]; Hamm et al.[6, 7]), and producing the annual catch and effort report series "Fishery Statistics of the Western Pacific" (Hamm et al., var. years[8]).

In addition to providing these support functions to the official WPACFIN agencies, the central WPACFIN program office has provided similar technical guidance and assistance to fisheries offices in other U.S. affiliated Pacific island areas such as the Federated States of Micronesia (Pohnpei, Kosrae, Chuuk, and Yap) and the Republic of Palau, but on a more limited basis. Notwithstanding the limited support provided, at least some "WPACFIN-compatible" data systems have been created in each of these other island areas.

The WPACFIN network refers to the technologies, activities, and meth-

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[1] CIC Research, Inc. 1983. A fishery data collection system: Guam. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-83–21C, 85 p.

[2] CIC Research, Inc. 1983. A fishery data collection system: Saipan. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-83–20C, 74 p.

[3] Omnitrak Research and Marketing Group, Inc. 1988. Sampling methodology for a boat fishing survey design for Hawaii. Honolulu, HI 96813, 173 p.

[4] Malvestuto, S. P. 1991. Recommendations for statistical treatment of Hawaii small boat survey data. Fishery Information Management Systems, Auburn, AL 36830, 6 p.

[5] Hamm, D. C., and M. M. C. Quach. 1988. Bottomfish fisheries of American Samoa, Guam, and the Commonwealth of the Northern Mariana Islands. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-88–15, 76 p.

[6] Hamm, D. C., M. M. C. Quach, R. Tokunaga, F. Aitaoto, G. W. Davis, and T. J. Donaldson. 1989. Review of the 1988 pelagic fisheries of American Samoa, Guam, and the Commonwealth of the Northern Mariana Islands. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-89–7, 101 p.

[7] Hamm, D. C., M. M. C. Quach, F. Aitaoto, G. W. Davis, and T. J. Donaldson. 1989. Review of the 1988 bottomfish fisheries of American Samoa, Guam, and the Commonwealth of the Northern Mariana Islands. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-89–8, 83 p.

[8] Hamm, D. C. et. al. 1986 Vol. I, 1986 Vol. II, 1988 Vol. III, 1989 Vol. IV, 1990 Vol. V, 1991 Vol VI, and 1992 Vol VII. Fishery Statistics of the Western Pacific. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent. Admin. Rep. H-86–4, 380 p., Admin. Rep. H-86–20, 237 p., Admin. Rep. H-88–4, 352 p., Admin. Rep. H-89–1, 216 p., Admin. Rep. H-90–09, 224 p., Admin. Rep. H-91–1, 230 p., Admin. Rep. H-92–06, 230 p.

odologies upon which the system functions, including all the hardware, software, communication links, data sharing capabilities, and the data bases themselves. The network is the backbone of WPACFIN, and is a physical part of each participating agency. In general, the network is a microcomputer-based means of sharing data and information among fisheries agencies to support fisheries management needs via mail and direct telecommunications. It is more fully described under the WPACFIN evolution section of this paper.

Together, these three aspects of WPACFIN, the organization, program, and network, make the WPACFIN system what it is, a combination of agencies working together in a voluntary and cooperative manner to improve fishery management capabilities in the central and western Pacific region.

## Problems and Challenges of Implementing WPACFIN

Implementing an information network among the U.S. affiliated islands of the Pacific required resolving some challenging problems and operating within certain strict limitations. Effective communication is important in any cooperative undertaking, but it is critical in a task such as developing and implementing WPACFIN. The first, and possibly most obvious obstacle limiting communication among participating agencies is the physical size of the area involved. The distances between the central WPACFIN office and the flag state agencies are great, and the Exclusive Economic Zones (EEZ's) are the largest under jurisdiction of any of the Councils, totaling over two million square miles (Fig. 2). To put the size of the area in perspective, if the central WPACFIN office was in Bangor, Maine, the American Samoa fisheries office would be in Venezuela and the Guam and Saipan offices would still be in the Pacific Ocean well west of California. The distances make costs of on-site visits high, and communication via telephone lines is also quite expensive; thus, overcoming the complications caused by the distances involved was no minor task, but progress was steadily made because of the high level of cooperation and commitment by the flag state agencies. On-site visits to the flag state agencies by central WPACFIN technical staff were well planned and always productive by concentrating a lot of activity into the few days available.

Cultural differences represent a second challenge in communication that is also somewhat related to the size of the area covered. The Samoan, Hawai-

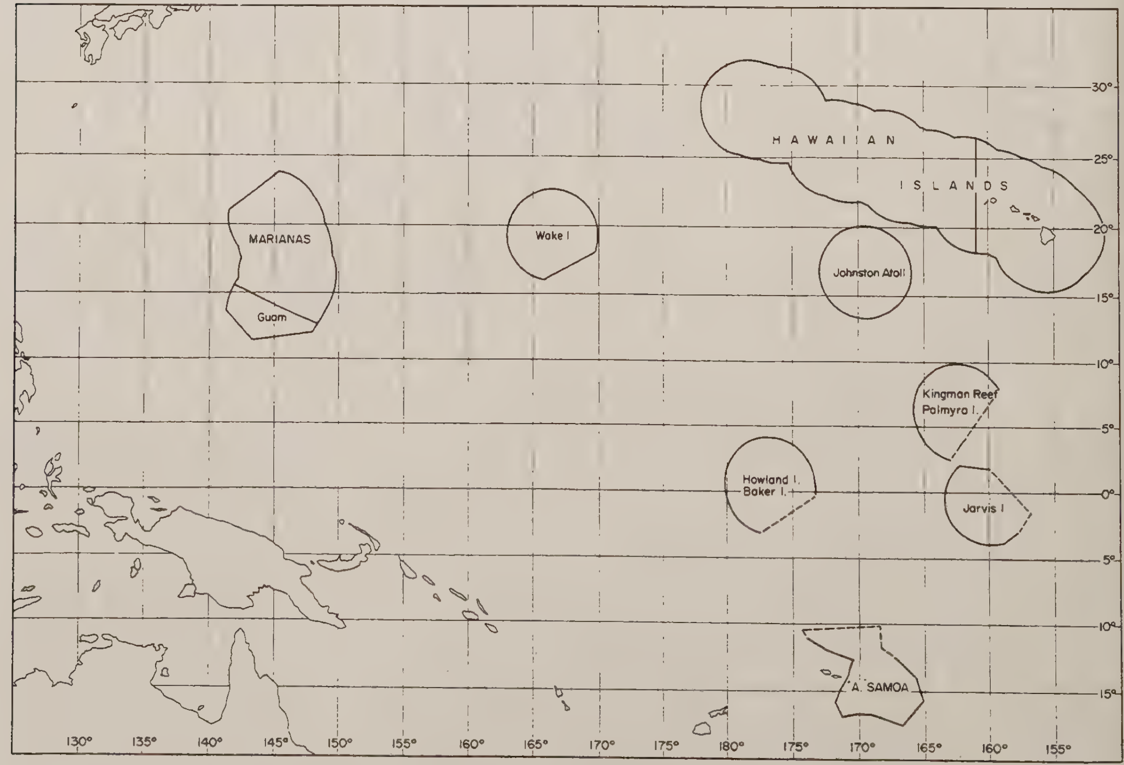

Figure 2.—Boundaries of the Fishery Conservation Zone around Hawaii, American Samoa, Guam, the Northern Mariana Islands, and other U.S. possessions.

ian, and Chamorro/Carolinian cultures are all quite different; even within the Chamorro/Carolinian cultures of Guam and the CNMI, differences exist between islands. Overcoming communication problems and understanding limitations related to cultural differences require sensitivity to and respect for local customs, preferences, inhibitions, attitudes, and sometimes underlying and significant prejudices. It requires time to build relationships, gain confidences, and understand the differences and nuances of each island culture. Not understanding or ignoring cultural differences reduces the effectiveness of communication and is likely to result in less functional and useful data systems. The WPACFIN philosophy embodies these cultural differences as much as possible in developing new or modifying existing data systems. Related to the cultural differences are political differences and stages of development of the bureaucracies of the island fisheries agencies; these too must be considered and overcome.

Several other complications in developing an automated fishery information network in the Pacific may be broadly categorized as infrastructure problems. In 1981, only the State of Hawaii possessed laws requiring the reporting of fisheries statistics. Therefore, historical data for the early years of most island fisheries were inadequate, as was available funding; voluntary reprogramming of available funds by the flag state agencies made implementing data system changes possible. Progress was also hindered by a lack of adequate staff. Fisheries and computer professionals are still very scarce in the Pacific, so the central WPACFIN office has had to provide nearly all computer training and programming support, at least to the flag state agencies. The American Samoa and CNMI offices rely almost exclusively on contract professional biologists from the U.S. mainland. As a result, a high level of turnover, low level of stability in programs, and a poor understanding of the history of the fisheries exist. The WPACFIN program has worked to help the island agencies overcome these problems.

The last noteworthy challenge in implementing and upgrading WPACFIN has been the dynamics of rapid changes in the fisheries, the data needs, and the computer technologies over the past decade. In the early years, fisheries managers required only a few summary tables and enough basic data to categorize the fisheries and document their importance for justifying and implementing fishery management plans. Now, more detailed annual reports are required that document status of the stocks aspects of fishery performance, and selected economic indicators. Fortunately, computer technology capable of handling the increased data and analytical needs has also expanded, but with the expansion has come a challenge of maintaining stability of systems while implementing significant improvements. This has been accomplished successfully in the flag state agencies where levels of cooperation were high and levels of bureaucracy and changes in the basic fisheries were fairly low, but less successfully in Hawaii where the reverse is true.

## WPACFIN Evolution

The discussion of the evolution of the WPACFIN system will be divided into the same three aspects of WPACFIN as previously described, the organization, program, and network.

The original members of the WPACFIN organization included all those shown in Figure 1, except the Guam Department of Commerce, which joined in August 1988. Initially, HDAR participation in the FDCC was self-limited to observer status, but in December 1984, with completion of the Hawaii statistical system study (DLNR[9]), they became a full voting member of the FDCC. The FDCC held ten meetings from 1982 to 1989 which mostly dealt with issues such as establishing memoranda of understanding and data share agreements, developing guidelines for operating the FDCC, implementing the first and second generation systems, and seeking additional funding to support the network. From 1989 to 1992, the FDCC met eight more times and concentrated its efforts on defining projects and objectives under the new PACFIN initiative, developing a long-term data plan for the Pacific, and redefining the functions, services, and data bases the future WPACFIN system should include. The FDCC's Technical Subcommittee has held several workshops and training sessions and has developed standard guidelines for data quality control and file management procedures to be used by each member agency in developing their own specific procedures to insure that only quality data enter the central WPACFIN files.

The WPACFIN program has been crucial to WPACFIN system development. Established in 1981 by the Southwest Fisheries Center as a separate task within the Honolulu Laboratory, it was initially staffed with one full-time computer systems analyst. Staff size and expertise expanded to improve WPACFIN capabilities in meeting overall fishery information and Council-related needs. Expertise in fisheries biology was transferred into WPACFIN to help with fisheries applications and analyses.

Discussion of the evolution of the WPACFIN network will be limited to the major hardware and software used and will be described in three sections, pre-WPACFIN, first generation WPACFIN, and second generation WPACFIN. Identification of the data bases maintained within the network is found in the next section.

The pre-WPACFIN situation was a fairly unstructured, low technology environment involving no computer use outside Hawaii. Fishery statistics in the flag states were computed by hand or sometimes with the use of desktop calculators. Data collecting systems, where they existed, were fairly rudimentary and typically were not based on valid statistical designs. Data processing at HDAR and the Honolulu Laboratory was performed by keypunch cards, batch processing, and limited time-share processing on state-operated IBM mainframe computers. Data exchanges were limited to periodic transfer of computer tapes from HDAR to the Honolulu Laboratory. The HDAR had over a two-year backlog of data to process.

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[9] Div. Aquatic Resources, State of Hawaii. 1984. Hawaii fisheries statistics system design study. Division of Aquatic Resources, Div. Land and Natl. Resources, 214 p.

The initial steps in implementing the first-generation WPACFIN system consisted of installing a two-station, key-to-disk data entry system at the Honolulu Laboratory and Apple II+ microcomputer systems in each of the original four participating island agency main offices plus central WPACFIN. These Apples were the first microcomputers introduced into any of the flag state agencies. The original off-the-shelf software included a highly structured, but somewhat limited, data base management system capable of all processing steps from data entry through report generation, a spreadsheet system, some rudimentary graphics and statistics packages, word processing, and some basic utilities. By the end of 1982 all island systems had been installed, basic training provided, and data bases established for the major fishery monitoring systems (Hamm[10]). Over the next several years, hardware and software upgrades continued to be made which included additional computers, networked hard drive units in two offices, and extensive custom-programmed processing systems for newly designed and implemented creel survey sampling programs in all flag state areas (Hamm[11]). Additional data bases and improved sampling programs were established in all flag state areas to monitor the resources better. The HDAR began reducing the backlog of landings reports and completed the WPACFIN-funded "Hawaii fisheries statistics system design study" (1984). Some of the newly designed sampling programs for the flag states (e.g., market sampling, size frequency and biological sampling, some creel surveys) were never implemented or were soon terminated because of lack of funds to conduct the work or because of a lack of demonstrated and reinforced need for these data for federal management purposes. This proved to be most unfortunate as these types of baseline data were later needed by Council Plan Monitoring Teams.

In addition to the Apple II+ hardware for processing centrally stored files, the first generation central WPACFIN hardware environment initially included a time-share link to a PDP 1170 minicomputer. However, the availability of the minicomputer proved to be short-lived, and the Laboratory obtained an in-house CPM-based multiuser-multiprocessor super-microcomputer with over 40 workstations which became the central computer for some WPACFIN applications. This fairly simple first-generation processing environment continued to meet data processing needs into the mid-1980's when it became apparent that a major switch to more modern and powerful processing equipment would soon be needed to meet the ever increasing federal requirements for more sophisticated analysis and reporting.

The evolution to second-generation WPACFIN processing systems began with the microcomputer boom of the mid-1980's.

Whereas most of the first-generation hardware and software systems were provided through central WPACFIN technical and financial support, the evolution to second-generation WPACFIN processing systems required much more financial commitment from the other participating agencies. This was partly accomplished through reprogramming existing Federal grant funds which had already been extensively used to implement improvements in data collecting systems, and partly through the use of other Federal and local funds. The new WPACFIN standard operating environment centered around the IBM-compatible MS-DOS microcomputer and the dBASE data base management system. The microcomputer revolution soon reached all participating agencies, and they began expanding their use of computers beyond their fisheries data sections to their fisheries biologists, and wildlife and administrative sections. The American Samoa DMWR, CNMI DFW, and Guam DOC offices followed the WPACFIN standard almost exclusively in their expansion efforts, but the Guam DAWR office chose to use the Apple Macintosh system and the HDAR office expanded in several directions simultaneously: into direct use of the IBM mainframe, a newly installed State WANGNET minicomputer system, and into increased use of both Macintosh and IBM-compatible microcomputers.

During the evolution to second-generation computer systems, the major emphasis of the central WPACFIN program was to support the conversion to the new IBM-compatible operating environment by assisting with purchases of hardware and software and by developing much more sophisticated and comprehensive, user-friendly, menu-driven dBASE applications for an increasing number of data collection and analysis systems. The most recent phases of implementing the second generation WPACFIN system include establishing direct computer-to-computer telecommunications links between the central office and all other agencies, and creating an on-line central system for dial-in access to principal island data sets. The evolution into the second-generation operating environment is continuing. As all the basic fisheries data systems become fully functional in the new operating environment, more emphasis will be placed on developing more integrated data systems and additional analysis, assessment, and reporting systems to enhance fisheries monitoring and management.

## Current Data Systems

NMFS and each of the four island areas have a variety of data bases and associated collecting and processing systems to facilitate fisheries monitoring and management activities (Table 1), but it is beyond the scope of this paper to document them fully. Each fishery, island agency, and data processing system has its own needs, peculiarities, uses, capabilities, and limitations that make it unique. In general, each agency is responsible for ensuring its data are as accurate as possible before sharing files through the central WPACFIN office. Most data collected by participating island agencies are centrally archived for ready access and data sharing in WPACFIN files at the Honolulu Laboratory. Most data collected by NMFS are maintained at the Honolulu Laboratory by the Fishery Management and Performance Investigation to reduce WPACFIN storage requirements. Not all data are readily available to all users because of confidentiality or sensitivity considerations, or because use of the data is local rather than regional.

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[10] Hamm, D. C. 1982. Preliminary description of the Western Pacific Fishery Information Network. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-82–2, 11 p.

[11] Hamm, D. C. 1985. Western Pacific Fishery Information Network, organization and design, status and issues. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-85–4, 35 p.

From a fisheries monitoring perspective, the most important systems in each island area are the commercial landings, creel survey, and logbook systems. Even though these systems vary significantly in design and degree of implementation from island to island and from system to system (e.g., voluntary vs. mandatory, on-site vs. mail-in, census vs. sample, and local agency vs. central WPACFIN sponsored), they provide the basis for monitoring fisheries of the area. The other data systems operated by fisheries agencies provide important validation cross-checks, biological status, augmentary, and ancillary information on the resources and fisheries exploiting them.

Table 1.—Data collecting and processing systems.

| System | NMFS | Samoa | Guam | CNMI | Hawaii |
|---|---|---|---|---|---|
| Commercial landings | | X | X | X | X |
| Offshore "creel" surveys | | X | X | X | X |
| Inshore "creel" surveys | | X | X | X | |
| "Tuna" transshipment | | X | X | X | |
| Vessel inventory | | X | X | X | X |
| Tournament sampling | | X | X | X | |
| Length/size sampling | X | X | X | X | |
| Biological sampling | X | X | X | X | |
| Permits and licenses | X | X | X | X | X |
| Imports and/or exports | | | X | X | |
| HI auction monitoring | X | | | | X |
| NWHI lobster logbooks | X | | | | |
| Longline logbooks | X | | | | |

## Future Goals of the WPACFIN System

During the past 11 years, significant progress has been made toward meeting fisheries management needs in each of the Pacific island areas under the Council's jurisdiction; however, much more remains to be done. Fisheries management information requirements continue to change, and significant data and information gaps still exist. Filling those gaps will require some reorientation of major activities within the WPACFIN system to implement further improvements in the methods of data collection, processing, analysis, and reporting. Some of the goals of the WPACFIN system for future activities are the following:

1) Analyze existing data systems to document information gaps.

2) Establish additional data collecting, processing, and analyzing standards, and implement changes required to meet those standards.

3) Implement computer-based telecommunications between all participating agencies to facilitate data exchange and system upgrades.

4) Establish dial-in access to centrally archived data bases.

5) Establish integrated central data bases and create a sophisticated query system to improve access to and use of available data.

6) Develop new and improved fisheries assessment and analysis systems to increase the reliability of information used in the fishery management decision making process.

7) Encourage further state and Federal cooperative efforts in meeting fishery management objectives in the western Pacific.

## Summary

Over the past 11 years the NMFS's WPACFIN program has assisted island fisheries agencies in advancing from nonexistent or rudimentary manual data systems to sophisticated computerized systems capable of providing useful fisheries monitoring and analysis information on a timely basis. Through the cooperative efforts of all participating agencies, the WPACFIN system has become the common thread that weaves the member agencies together through sharing data and information about the fisheries of the Pacific in their efforts to protect and manage these resources.

Several critical factors have been identified which influence the level of success obtainable in implementing a complex, intergovernmental, voluntary, and cooperative project such as this fishery information network:

1) Commitment and ability of agencies to implement changes and provide resources to accomplish change.

2) Long-term commitment and quality of individual employees involved in the project, especially those involved in project management.

3) Consideration of local needs, culture, politics, capabilities, limitations, and personnel.

4) Continual contact, support, feedback, and training.

As fisheries change and fisheries management needs grow in complexity and diversity, so must the resolve of the participating agencies grow to meet the new challenges. The most important factor influencing the future of the fisheries of the Pacific will continue to be the desire and the ability of the many agencies to work together to become a unified force in meeting the challenges of rational and effective fisheries management. It is the long-term goal of the WPACFIN system to assist in making effective management a reality. The WPACFIN system continues to evolve to meet needs of rapidly changing fisheries management requirements.

9342

STATE OF CALIFORNIA
THE RESOURCES AGENCY
DEPARTMENT OF FISH AND GAME

FISH BULLETIN 175

# THE CALIFORNIA DRIFT GILL NET FISHERY FOR SHARKS AND SWORDFISH, 1981-82 THROUGH 1990-91

*by*

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*Southwest Fisheries Science Center*

1993

## ABSTRACT

California's drift gill net fishery developed rapidly in the late 1970s off southern California. The fishery originally targeted the common thresher *Alopias vulpinus*. Almost immediately swordfish *Xiphias gladius* and shortfin mako *Isurus oxyrinchus* became important components of the catch.

We examined and summarized data obtained from the California logbook system, landing receipts, and market samples taken from this fishery over the 10 fishing seasons from 1981-82 through 1990-91. During this period the fishery evolved from a small nearshore experiment to a major California fishery. Significant changes in nearly every aspect of the fishery occurred including boats and gear, techniques and regulations, fishing areas and seasons, and targeted species. These data form a base line from which changes in the fishery and harvested stocks can be compared in the future.

The drift gill net fishery operates primarily in the area between San Diego and Cape Mendocino and concentrates much of its effort on swordfish in the Southern California Bight during the months of May to December. During the period studied, fishing effort decreased 50% to 60%, from highs of approximately 11,000 sets to a low of about 4000 sets in the 1990-91 season. This decrease in effort corresponds to a decrease in total landings of approximately the same proportions. Decreases in landings of common thresher were over 80%, while swordfish and shortfin mako landings decreased 60% and 40% respectively. Average sizes of swordfish showed no change during the 1981-82 to 1990-91 fishing seasons. Average sizes of shortfin makos showed a decrease of approximately 40% from the 1982-83 through the 1985-86 fishing season, but rebounded during the 1989-90 season to within 15% of the 1982-83 season. Average sizes of common thresher, however, decreased 30% from the 1982-83 season and remained low. This may indicate a decline in the common thresher stock or reflect changes in the season and area of fishing operations.

A number of problems and conflicts occurred during the first 10 years of the fishery (e.g. bycatch of marine mammals and striped marlin *Tetrapturus audax*) which were resolved for the most part through the cooperative efforts of the commercial industry, the sport industry, environmental groups, and State and Federal governments. The incidental catch of marine mammals is apparently low and not compromising any stocks, although the potential for damage remains and therefore monitoring is prudent. Bycatch of other fishes does not appear to be a problem except for the catch of blue sharks *Prionace glauca*, which has an unknown affect on local stocks.

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# INTRODUCTION

California's drift gill net fishery for pelagic sharks and swordfish *Xiphias gladius* developed in the late 1970s off southern California. The initial concept of catching large pelagic sharks was inspired by the occasional catch of sharks in gill nets used to drift near shore for California barracuda *Sphyraena argentea* and white seabass *Atractoscion nobilis*. The fishery evolved rapidly as fishermen modified coastal gill nets and techniques for catching white seabass, sharks, California halibut *Paralichthys californicus*, and California flyingfish *Cypselurus californicus*.

The successful development of the drift gill net fishery might be attributed to greater fuel efficiency than in some other fisheries, pelagic shark resource abundance, consumer acceptance of shark as a food fish, and the perseverance of fishermen pursuing a new source of livelihood. As fishing techniques and gear improved, market demand for sharks increased, and in less than 5 years the number of drift gill net permits grew to over 200. These shark fishermen soon discovered that the nets were also efficient at catching swordfish, worth nearly four times the dockside value of sharks (Bedford 1987; Holts 1988). The value of swordfish and market demand for the high quality, relatively inexpensive sharks encouraged further development; fishermen started exploring new areas farther offshore and northward off Oregon and Washington.

As the fishery expanded, conflicts emerged with the commercial harpoon fishery for swordfish and with the recreational hook-and-line fishery for striped marlin *Tetrapturus audax* and swordfish, though few swordfish were caught by hook and line. Commercial harpoon fishermen and recreational fishermen feared reduced availability of swordfish and striped marlin. Additionally, striped marlin were specifically reserved for the recreational fishery and could not be sold even if caught incidentally. Another bycatch problem that developed was the incidental catch of marine mammals (Hanan and Scholl 1985; Diamond et al. 1986, 1987), especially California sea lions *Zalophus californianus*, which were caught in large numbers in drift gill nets near the Channel Islands. Because of these conflicts, concern for the targeted fish resources (Hanan 1984), and the fact that very little was known about the population status or biology of thresher sharks *Alopias* spp. (Berkson 1985), the Legislature enacted a series of laws regulating the new fishery (Bedford 1987).

In this bulletin, we review the first 10 years of the California drift gill net fishery, including a fishery description, catch and fishing-effort summaries, regulations, and biological summaries.

# THE FISHERY

The drift gill net fishery originally targeted common thresher *Alopias vulpinus* and shortfin mako *Isurus oxyrinchus* (locally known as bonito shark). Almost immediately swordfish became an important component of the catch. Additionally, some other unexpected or previously considered rare species were caught. These included two other thresher shark species, bigeye thresher *A. superciliosus* and pelagic thresher *A. pelagicus*[1]. Fishermen and fish buyers learned what was marketable and in some cases developed markets for fishes not previously available in commercial quantities (e.g. opah *Lampris guttatus* and louvar *Luvarus imperialis*). The bycatch of nontarget fishes varied by year, but some of the more predictable and saleable bycatches were albacore *Thunnus alalunga* and other tunas, Pacific bonito *Sarda chiliensis*, and white seabass (Table 1).

During the period reviewed, primary ports for the drift gill net vessels were San Diego, San Pedro, and Santa Barbara; additionally, some boats utilized Dana Point, Port Hueneme, Ventura, Port San Luis, Morro Bay, Monterey, Moss Landing, and San Francisco Bay area ports. Depending on where they were fishing, drift gill net boats landed fish at all of these ports as well as several others.

Fish availability, market price, weather conditions, vessel fishing range, and fish-cooling capabilities dictated the length of fishing trips. Drift gill net trips ranged from one night to one month and total trips per year varied widely by skipper. Some skippers made only short trips while others remained at sea 2 to 3 weeks or more (Diamond et al. 1986). After extended trips or when catch rates were low, fishermen often docked at ports other than their home port to allow for shore leave or to wait for improved fishing conditions. Often they were gone from home port several months, returning only to change fishing gear for the opening of a different fishery.

Areas of operation for the drift gill net fishery were the nearshore banks, canyons, and escarpments near the offshore islands (water depths ranged from 400 to 1000 fathoms [fm]; Figures 1 and 2). Gradually, as the fishery matured and larger vessels entered the fishery, operations moved offshore and northward to the more distant seamounts and to the edge of the continental shelf. During and among fishing seasons, fishing areas shifted depending on availability of targeted fish and legislated time and area closures. Fishing effort varied from season to season and peaked in the mid-1980s (Figure 3).

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[1] *Although this species has not been previously reported in California waters, three California Department of Fish and Game observers including one of the authors (Hanan) identified this species in the observed catch. Pelagic threshers were also reported and measured by CDFG samplers at the docks as the sharks were offloaded. Unfortunately, no specimens were photographed or retained.*

Using radios, some fishermen communicated in coded messages with other members of loosely formed organizations called "code groups." They shared location information and presence or absence of desired fish. When catch rates were low, code-group members spread throughout the fishing range in search of fish and kept each other informed of fishing conditions, catch rates, and other pertinent information. Often, fishing vessels moved rapidly from one area to another based on information from their code group.

Because of competition for available fish and code-group loyalty, airplanes were hired to observe catches of other code groups. To counter this spy tactic, fishermen sometimes covered their catch with tarps or created fake fish by leaving a fish head protruding from under a tarp. Sometimes pilots would throttle back their engines and glide over a fishing boat in hopes of covertly gaining information.

In the first few years of the fishery, most of the fishing vessels were wooden or fiberglass; gradually there was a transition to steel or aluminum as the fishery developed. Vessel size ranged from 30 to 75 ft. Average vessel size increased with time, especially for those fishing farther offshore and northward. Fish holds were generally below decks and capacity varied depending on boat size and configuration. Fish-cooling capabilities varied widely from none to ice, brine spray, or refrigeration.

Crew size ranged from one to six. Crew members were compensated usually with a share of the catch proceeds or sometimes with cash wages. When shares were used as compensation, often they were split in some combination of the following: a share to the owner, a share to the skipper, a share or shares to the boat (for food, fuel, and other overhead), a share for each crew member, and sometimes one for the permit holder, who may or may not have been one of the aforementioned.

Drift gill net permits were issued to individual fishermen rather than to boats; thus the value of boats did not become artificially inflated, and permit holders could buy new boats as needed. Because of a requirement that a permit holder be onboard during fishing operations, some permit holders would "hire out" (ride for cash or a share) on other fishing vessels for skippers who did not have a permit. The practice of hiring out was eliminated in 1980 by requiring permit applicants to declare on which fishing vessel they would be using the permit. Also in 1980, the legislature made the drift gill net fishery a limited entry fishery, setting a maximum number of permits and allowing those already involved to continue fishing. The number of drift gill net vessels may have been as high as 300 in 1985, but there were rarely more than 100 active vessels during any of the fishing seasons described here.

TABLE 1. Landings (lb) by California drift gill net vessels during the 1981-82 through 1990-91 fishing seasons, compiled from landing receipts. Data for 1990-91 are preliminary. Some landings reported here are of species (i.e. angel sharks) not usually caught by drift gill net vessels, but have been included because they were reported on landing receipts.

| Species | 1981-82 | 1982-83 | 1983-84 | 1984-85 | 1985-86 | 1986-87 | 1987-88 | 1988-89 | 1989-90 | 1990-91 |
|---|---|---|---|---|---|---|---|---|---|---|
| Sharks[a] | | | | | | | | | | |
| Angel shark, Pacific | 2,551 | - | 10,172 | 1,210 | 1,049 | 358 | - | 107 | - | - |
| Blacktip shark | - | - | - | 440 | - | - | - | - | - | - |
| Blue shark | 27,642 | 7,253 | 4,943 | 278 | - | 1,056 | 1,086 | 226 | - | 65 |
| Cow shark | - | - | 36 | 523 | - | - | - | - | - | - |
| Dogfish, spiny | - | 1,663 | - | - | 71 | - | 44 | - | 9 | 2 |
| Dusky shark | - | - | 174 | - | - | - | - | - | - | - |
| Hammerhead shark | 2,038 | 904 | 31,515 | 4,493 | 2,373 | 4,170 | 1,244 | 129 | - | 1,481 |
| Leopard shark | 540 | 348 | 608 | 290 | 189 | 78 | 60 | 400 | 211 | 72 |
| Mako, shortfin | 245,725 | 507,420 | 283,810 | 169,978 | 175,918 | 333,696 | 284,134 | 135,388 | 165,298 | 317,722 |
| Salmon shark | - | 996 | 66 | - | 1,169 | 960 | 135 | 265 | 179 | - |
| Sevengill shark | 104 | - | - | 104 | - | - | - | - | - | - |
| Smoothhound, brown | 6,084 | 3,779 | 2,927 | 164 | 13 | 2,600 | 2,170 | 6,205 | 1,675 | 1,447 |
| Smoothhound, gray | - | 422 | 57 | 16 | - | 343 | - | - | - | - |
| Soupfin shark | 28,251 | 11,855 | 6,878 | 10,788 | 8,708 | 2,346 | 4,937 | 2,725 | 2,224 | 2,238 |
| Thresher, bigeye | - | 34,197 | 85,965 | 59,320 | 102,648 | 39,773 | 23,022 | 8,563 | 20,116 | 38,192 |
| Thresher, common | 2,172,649 | 2,020,642 | 1,367,220 | 1,180,683 | 1,167,282 | 452,685 | 465,638 | 503,309 | 426,358 | 456,845 |
| Thresher, pelagic | - | - | 11,070 | 11,391 | 640 | 127 | 2,184 | 772 | 249 | 1,632 |
| White shark | - | - | 28 | 45 | 266 | 433 | 245 | 150 | 52 | - |
| Shark, unspecified | 232,736 | 14,482 | 19,130 | 6,350 | 8,362 | 1,351 | 448 | 333 | 1,180 | 1,139 |

TABLE 1. (Continued.)

| Species | 1981-82 | 1982-83 | 1983-84 | 1984-85 | 1985-86 | 1986-87 | 1987-88 | 1988-89 | 1989-90 | 1990-91 |
|---|---|---|---|---|---|---|---|---|---|---|
| Other fishes | | | | | | | | | | |
| Albacore | 1,135 | 16,068 | 104,803 | 175,223 | 228,838 | 202,792 | 136,161 | 80,478 | 28,110 | 22,528 |
| Barracuda, California | 17,502 | 14,477 | 1,173 | 382 | 1,077 | 4,176 | 126 | 1,596 | 515 | 679 |
| Bonita, Pacific | 26,004 | 20,937 | 32,026 | 5,944 | 1,845 | 7,115 | 10,307 | 812 | 2,705 | 1,503 |
| Butterfish, Pacific | 66 | 329 | - | 15 | - | - | 18 | 7 | - | - |
| Dolphinfish | - | 49 | 70 | - | 164 | 714 | 66 | 105 | 12 | 98 |
| Louvar | - | - | - | 10,808 | 20,811 | 8,186 | 7,779 | 4,292 | 5,992 | 9,470 |
| Mackerel, jack | 4,489 | 6 | - | - | - | - | - | - | - | - |
| Mackerel, Pacific | 10,698 | 2,246 | 438 | 11 | 220 | 2,025 | 432 | 438 | 158 | 602 |
| Mackerel, unspecified | - | 1,512 | 291 | 3,228 | 1,099 | 1,909 | 107 | 137 | 396 | 42 |
| Opah | 1,735 | 57,896 | 163,840 | 260,934 | 242,174 | 139,678 | 60,506 | 47,675 | 100,461 | 80,079 |
| Sardine, Pacific | - | - | - | - | - | 84 | 122 | - | 25 | 83 |
| Seabass, white | 97,547 | 2,812 | 2,196 | 1,156 | 3,356 | 4,837 | 485 | 2,337 | 527 | 4,524 |
| Sheephead, California | 182 | 212 | 369 | 30 | - | - | - | - | - | - |
| Swordfish | 707,729 | 1,533,971 | 2,517,352 | 3,387,829 | 3,054,303 | 2,708,092 | 1,804,611 | 1,631,182 | 1,685,734 | 1,504,894 |
| Tuna, bigeye | 1,868 | 3,524 | 17,026 | 5,804 | 3,646 | 8,378 | 9,549 | 10,603 | 849 | 1,394 |
| Tuna, bluefin | 937 | 1,375 | 2,827 | 7,681 | 4,556 | 4,959 | 2,031 | 3,798 | 5,509 | 17,479 |
| Tuna, skipjack | - | 22 | 25,354 | 12,465 | - | - | 571 | - | 9,953 | 1,907 |
| Tuna, yellowfin | 7,933 | 9,372 | 33,059 | 21,917 | 15,694 | 16,496 | 5,808 | 3,049 | 2,151 | 2,724 |
| Tuna, unspecified | 12,753 | 33,757 | 43,665 | 1,923 | 782 | 6,937 | 8,358 | 3,949 | 8,129 | 3,364 |
| Wahoo | - | 41 | - | - | - | 10 | 90 | - | - | - |
| Yellowtail | 28,474 | 838 | 1,418 | 1,188 | 2,136 | 3,592 | 1,092 | 2,728 | 159 | 1,419 |
| Totals | 3,637,372 | 4,303,405 | 4,770,506 | 5,342,611 | 5,049,389 | 3,959,956 | 2,833,566 | 2,451,758 | 2,468,936 | 2,473,624 |

[a] *The occurence of some of these species within the range of the California drift gill net fishery is unconfirmed. Published landing figures (Oliphant et al. 1990) have included several of these species under "Sharks, miscellaneous" or, in the case of pelagic thresher, under "Shark, common thresher."*

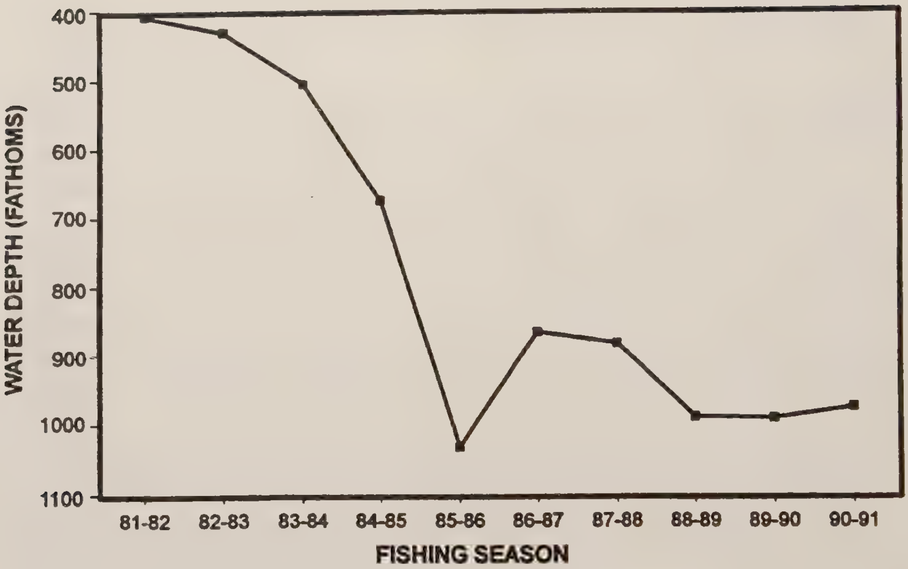


FIGURE 1. Average water depths (fathoms) fished by California drift gill net vessels for the 1981-82 through 1990-91 fishing seasons.

There was some illegal fishing (e.g. fishing without permits, use of excessively long nets, and other violations), but the value of the vessels and gear, combined with an active state enforcement program and costly penalties (e.g. the boat, net, and/or catch were subject to seizure and sale by court order upon conviction), discouraged the more blatant illegal activities.

## Gear and Fishing Operations

The visual characteristics of this fleet were distinctive. Often, 50 or more vessels fished within several miles of each other and at night could be identified by their bobbing, weaving mast lights. During the day they were more difficult to locate, but once sighted they were striking with the large net reel behind the cabin, the metal net or propeller guards raised above the stern, and the colorful bumper-ball floats stored along the wheelhouse (Figure 4). The net guards had the look of a large baseball catcher's mask or the face guard on a football helmet. Most drift gill net vessels employed a hydraulic or electric winch and boom for lifting the catch into or out of the hold and occasionally to assist in bringing aboard large fish.

Some skippers had previously harpooned swordfish and when issued a drift gill net permit were called dual permittees. In addition to net gear, their vessels

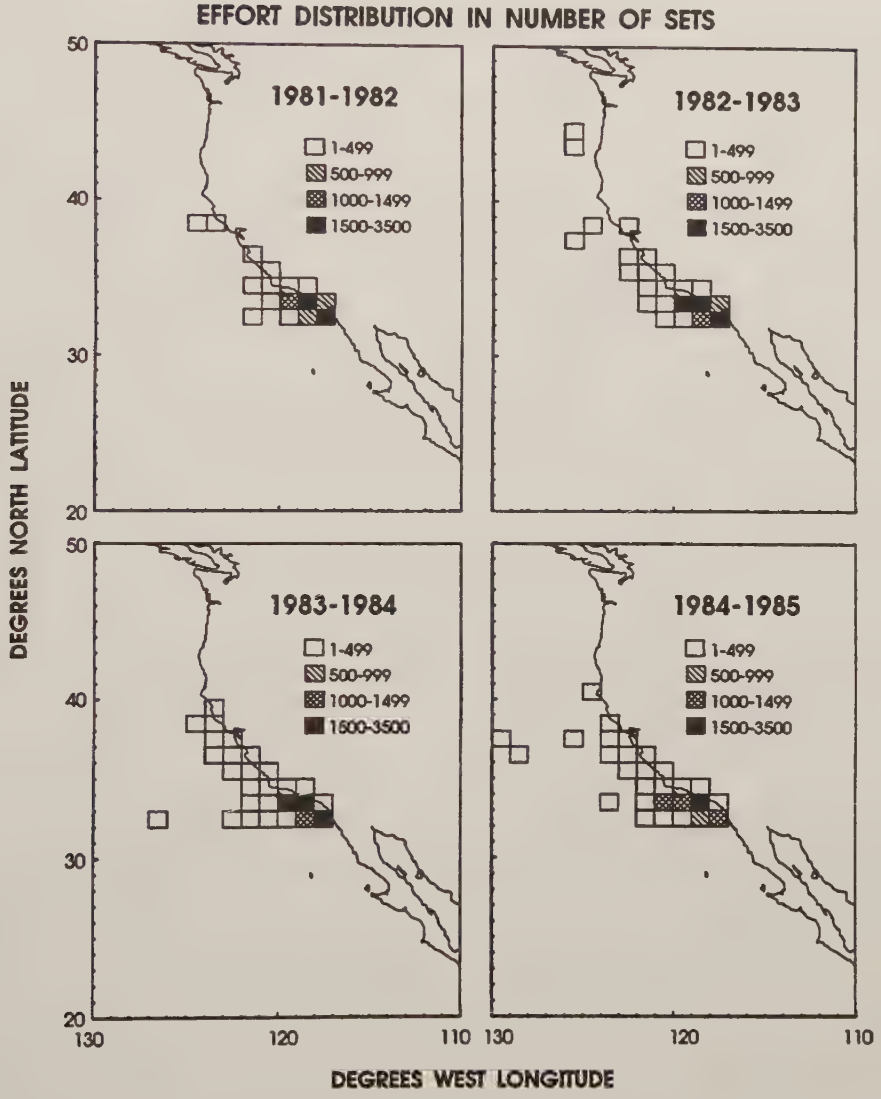

EFFORT DISTRIBUTION IN NUMBER OF SETS
1981-1982
1982-1983
1983-1984
1984-1985
1-499
500-999
1000-1499
1500-3500
50
40
30
20
130
120
110
DEGREES NORTH LATITUDE
DEGREES WEST LONGITUDE

FIGURE 2a. Distribution of fishing effort by 1° quadrangles in number of sets, from California drift gill net logbook data for the 1981-82 through 1984-85 fishing seasons.

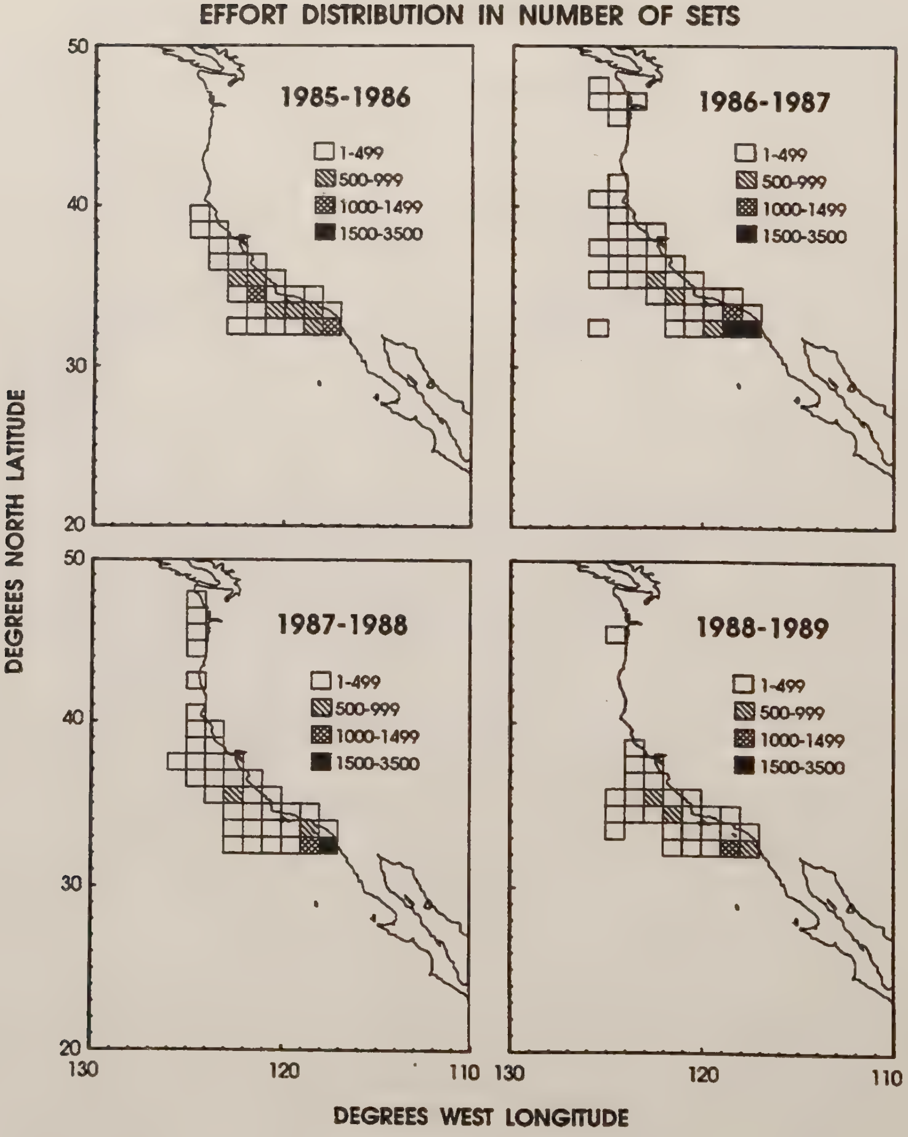

EFFORT DISTRIBUTION IN NUMBER OF SETS
1985-1986
1986-1987
1987-1988
1988-1989
□ 1-499
▨ 500-999
▩ 1000-1499
■ 1500-3500
DEGREES NORTH LATITUDE
50
40
30
20
DEGREES WEST LONGITUDE
130
120
110

FIGURE 2b. Distribution of fishing effort by 1° quadrangles in number of sets, from California drift gill net logbook data for the 1985-86 through 1988-89 fishing seasons.

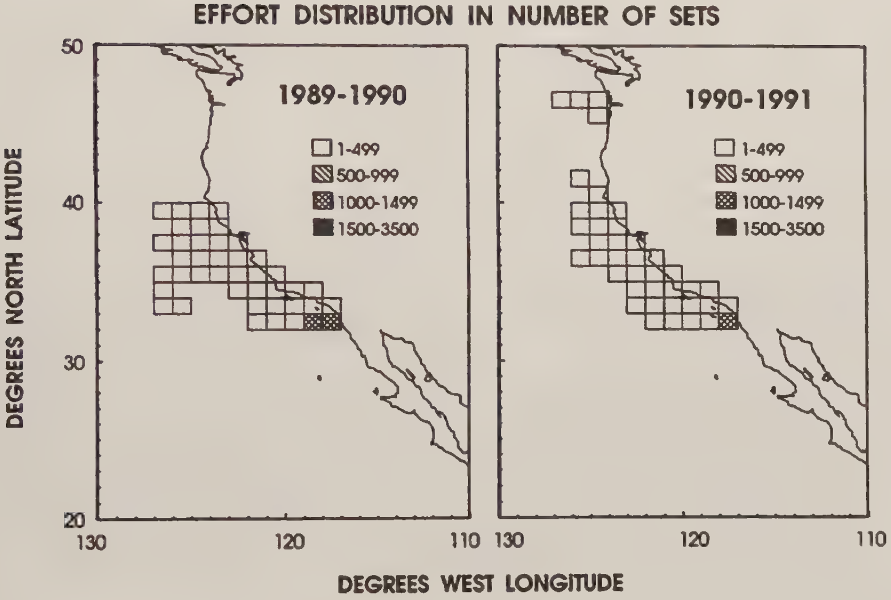


FIGURE 2c. Distribution of fishing effort by 1° quadrangles in number of sets, from California drift gill net logbook data for the 1989-90 and 1990-91 fishing seasons.

had wooden or metal planks extending 10 to 15 ft beyond the bow ending in a bow pulpit. Fishermen harpooned swordfish from the pulpit using harpoons tipped with a metal dart ("lily iron") designed to detach from the harpoon after striking the fish. The dart was attached by a line to large floats, and after striking a fish, the floats were released to tire the fish and keep it at the surface for later retrieval. Some vessels had a crow's nest high above the deck from which a fisherman could spot fish, direct the harpooner, and often steer the boat (Bedford and Hagerman 1983).

Nets used in the drift gill net fishery (Figure 5) ranged from 800 to 1000 fm in length. They were constructed of 3-strand, #24 to #30 twisted nylon tied to form meshes. The net was attached to the float line by means of a hanging line laced through two to four meshes of the top of the net and tied at intervals of 8 to 24 inches along the float line (Figure 5 detail). The number of meshes per hanging determined the amount of slack or tautness of the net and varied widely among skippers. The number of meshes between the cork and lead lines (depth of net) varied from 50 to 100 meshes depending on the skipper's preference. Average mesh size varied from about 13 to 19 inches stretched (Figure 6a).

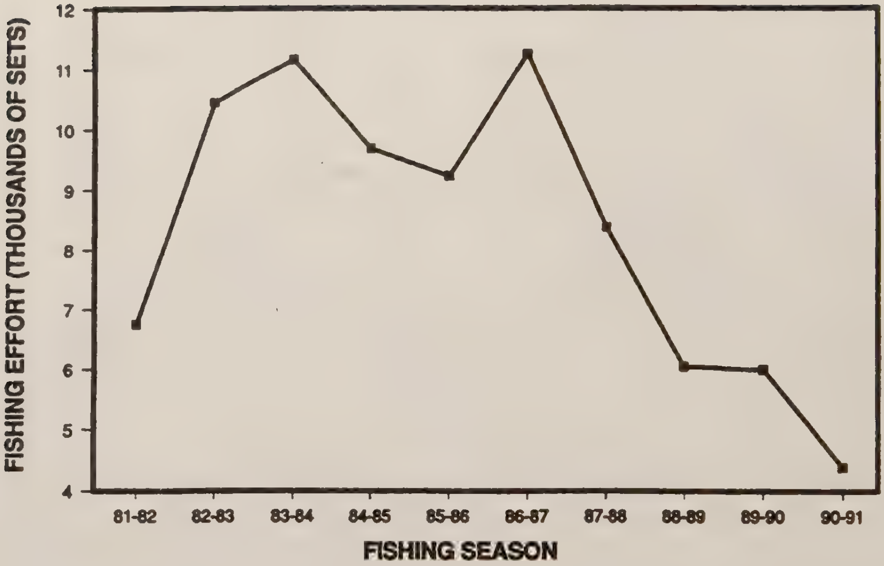


FIGURE 3. Estimated fishing effort in number of sets for California drift gill net vessels by fishing seasons 1981-82 through 1990-91.

Drift gill nets were usually fished with the float line 18 to 26 ft below the surface (Figure 6b) to allow small boats to pass over them. Fishing depth was maintained by tying buoy lines from the float line to bumper-balls at regular intervals of about 60 ft. The bumper-balls floated at the surface to buoy and maintain the net at a desired depth below the surface (Figure 5). The buoy lines were occasionally lengthened to as much as 90 ft when the skipper anticipated targeted fish to be at greater depths. A radar reflector and strobe light on a 6-ft pole was required at the end of the net. The reflectors allowed other boats to detect and avoid the nets and facilitated enforcement of maximum net lengths by patrol boats or airplanes. The bumper-ball floats, also visible on radar, showed the effect of currents and wind on net layout.

The nets were usually deployed or set each evening and usually only one or two people were needed. Deployment started by tossing the radar-reflector buoy overboard. The buoy was attached to the net via several fathoms of line followed by a length of netting sufficient to cause drag. The vessel was driven forward slowly as the net was payed out using the forward momentum of the boat and hydraulic-reel braking to control the speed of deployment. The buoy lines to the bumper-ball floats were snapped to the float line as the net was payed out. To

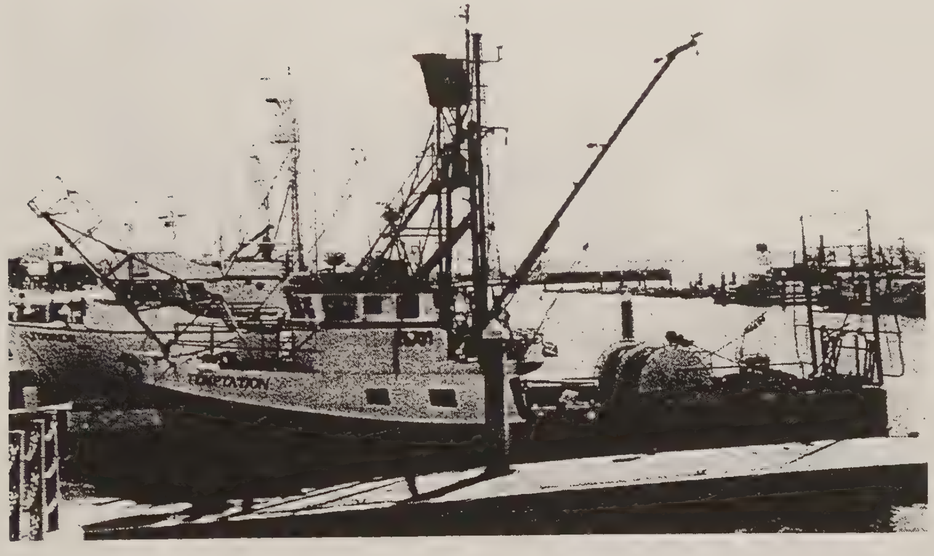


FIGURE 4. California drift gill net vessel with swordfish plank and pulpit at the bow, crow's nest atop the mast, net reel amidships, and net guard raised above the stern.

attract swordfish and increase the catch, many fishermen also attached chemical light-sticks to the net as it was payed out.

The nets were often set perpendicular to currents or across temperature, salinity, or turbidity fronts, because the fish tended to swim along those fronts. Each skipper seemed to choose the area to be fished based on a different set of criteria (e.g. some would not fish during a full moon, others tried to set in water of a particular color, and some tried to set on or near surfacing bait). In general, they tended to fish banks and escarpments which were also productive areas for bait and other fish.

The vessel remained attached to one end of the net while fishing, although sometimes it was detached and moved to the opposite end to change the drift pattern or fishing characteristics. Occasionally, if a net got too close to shore or the vessel drifted back over its net (putting a twist in the net and reducing its fishing capability), the skipper would pull and reset the net.

Nets were fished an average of 9 h. The net was pulled each morning with net pull taking 2 to 4 h. Because the whole net was required to be out of the water by 2 h after sunrise, the time at which a skipper would start the net pull differed depending on expected catch, length of net, duration of net pull, and time of year.

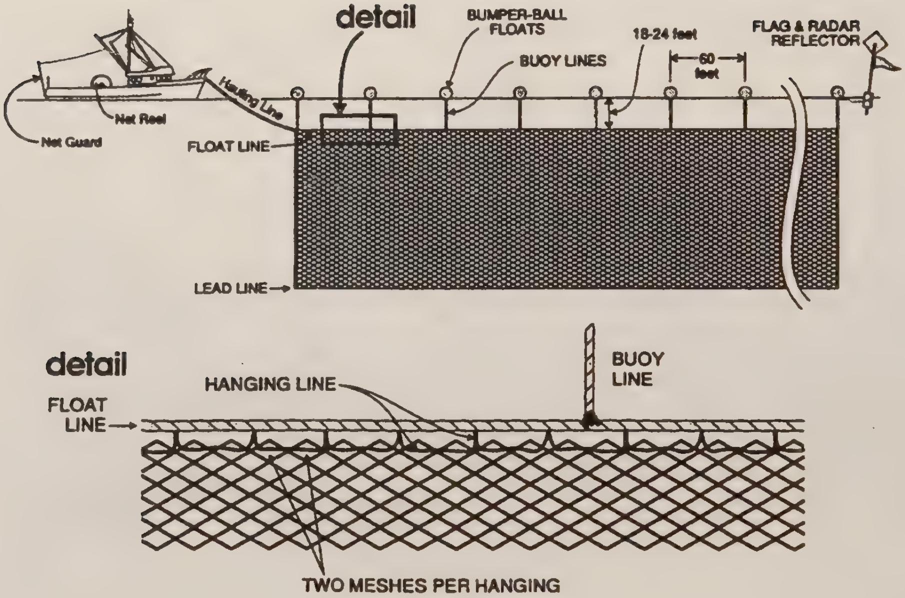

detail
BUMPER-BALL FLOATS
18-24 feet
FLAG & RADAR REFLECTOR
BUOY LINES
60 feet
Hauling Line
Net Reel
Net Guard
FLOAT LINE
LEAD LINE
detail
HANGING LINE
BUOY LINE
FLOAT LINE
TWO MESHES PER HANGING

FIGURE 5. Design of typical net in California drift gill net fishery.

The start of a net pull was often between 0100 and 0300 h, ending around sunrise. Net retrieval usually required all hands, each working on a particular task. The net guard was lowered over the stern to keep the net out of the propeller while it was pulled over the stern by the hydraulic net reel. In effect, this caused the boat to be pulled backward until late in the net pull, when the drag of the boat exceeded the drag of the net. Some vessels had rollers on the stern over which the net passed, thus facilitating retrieval and reducing net wear. Most vessels also used vertical guides to direct the net evenly from side to side on the net reel in much the same way as fishing line is wound on a fishing reel. Between sets, the net was stored on the reel, often covered with a tarp.

Most vessels had a secondary control panel (flying bridge), with engine throttle and net reel hydraulic controls, near the stern. As the net was pulled, anything caught in the net was usually seen coming to the surface; the reel was slowed and stopped if the catch was large. The catch was either pulled aboard in the net or, if too large, tied with a line so as not to be lost, and winched aboard.

Once onboard, entangled fish were removed from the net using routine procedures. Shark fins were cut off before removal. With thresher sharks, the tail, which was nearly as long as the body, also was cut off. Swordfish were removed by first

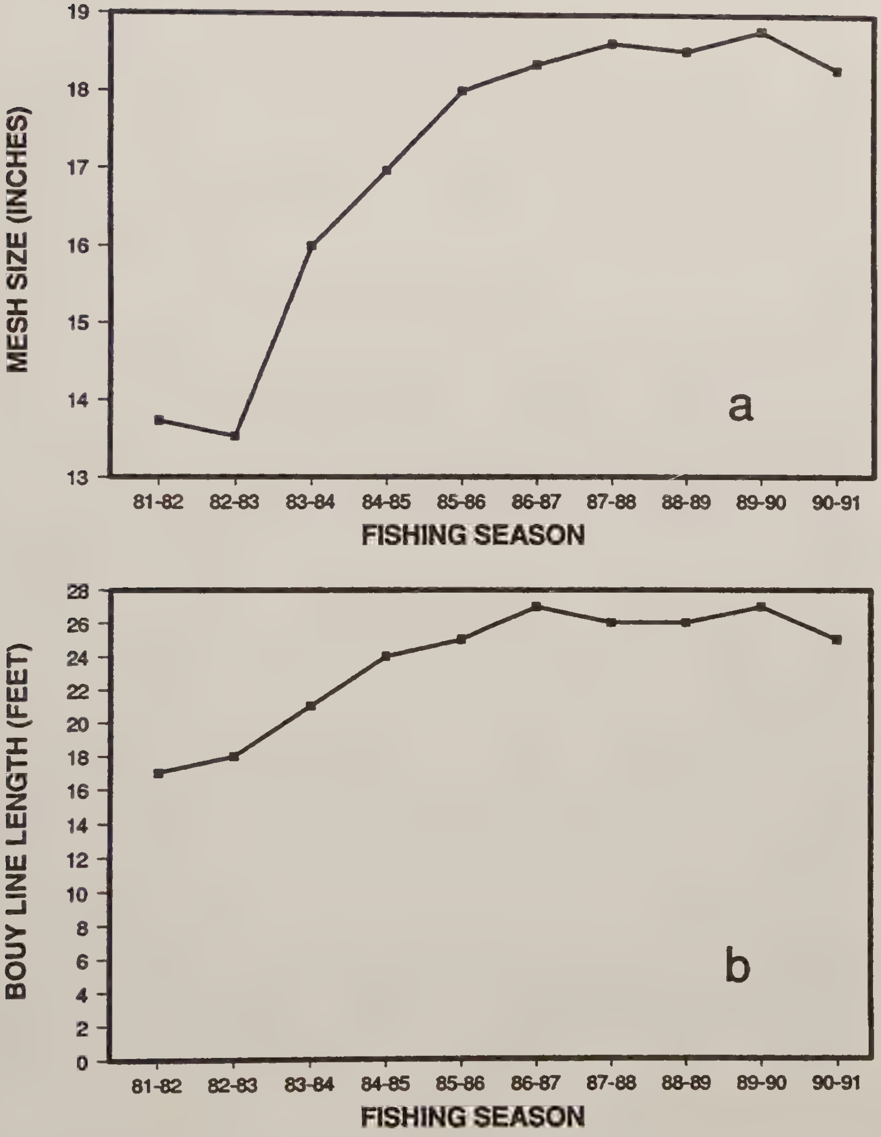


FIGURE 6. Average mesh size in inches (a) and buoy-line length in feet (b) used by California drift gill net vessels during the 1981-82 through 1990-91 fishing seasons.

sawing off the bill or "beak" and then removing the fins. One or more strands of the netting were sometimes cut to remove the entangled catch, but usually only as a last resort and often only with the skipper's permission, since holes in the net reduced fishing capacity and required repair at a later time. Depending on the number of fish caught or the rate at which they were coming aboard, the catch was either cleaned immediately or stacked on deck to be cleaned later. Cleaning of sharks and swordfish included head removal and evisceration. The unwanted parts were discarded at sea and the carcasses washed with sea water. Usually the thin belly meat (belly flaps) was discarded, although the crew would sometimes cook and consume this part. Some skippers kept the shark fins for drying and sale, but most discarded them. If the hold was large enough, shark carcasses were stored separately from swordfish to maintain swordfish quality.

Some fish became entangled early during a set, while others were entangled later or during the net pull. There were no trends in catch locations in the net relative to distance from the fishing vessel or to depth between the cork and lead lines. Except for blue sharks *Prionace glauca*, molas *Mola mola*, and pelagic sting rays *Dasyatis violacea*, most fish were dead when pulled aboard. Blue sharks often swam near or even through the netting as it was retrieved, accounting for many of them being alive when pulled aboard. Since blue sharks are unpredictable and likely to bite, they were usually clubbed immediately, removed from the net, and discarded on the down-current side of the net. The molas were thrown back alive, although sometimes they were kept until completion of the net pull to avoid reentanglement, a frequent occurrence with molas. Pelagic sting rays were removed and immediately tossed overboard. It was common for their tail barb to be hooked in the net, and often just barbs were found indicating they had freed themselves prior to net retrieval.

Marine mammals tended to roll up in the net when caught. Usually a few strands of the net had to be cut to remove them. Most sea lions and seals were dead when retrieved. Those still alive were released at the water line when possible or killed, removed from the net, and discard. If a marine mammal was too large for the hydraulic equipment to pull aboard, it was cut free at the water line.

## Catch

Catches varied by fish species, by season, and among years. Depending on the season and year, one set could yield as many as 15 swordfish, 20 shortfin makos, 20 thresher sharks, and 20 opahs, although many sets caught no marketable fish. Fish buyers often paid a prearranged price for the fish and often had agreements to buy all or a prearranged portion of the catch from a particular vessel. Most of the catch was sold in local markets (Herrick and Hanan 1988). Ex-vessel prices ranged from about $2.00 to $4.00/lb for swordfish, $1.00 to $2.00/lb for shark, and $0.25 to $0.50/lb (round weight) for opah. During the 10-year period covered in this study, mean annual landings were 2 million lb of swordfish, 1 million lb of common thresher, 40,000 lb of bigeye thresher, 3000 lb of pelagic thresher, and 262,000 lb of shortfin mako shark. Average landings over the last 5 years were quite close to the 10-year average, although there were declining trends in the total catch landed for most species (Table 1).

## Effort

Fishing effort used in this study was obtained from skippers' logbooks. Compliance with logbook reporting regulations was estimated to have been greater than 90% (Miller et al. 1983; Beeson and Hanan 1991), therefore total effort estimates based on logs was assumed to be accurate. Other studies have combined logbook information with landing receipt information to improve estimates of effort (Beeson and Hanan 1991); however, to evaluate effort trends we used only the logbook data.

During the 10-year period covered in this study, the annual distribution of effort in the drift gill net fishery shifted geographically from concentration in the nearshore Southern California Bight to more even distribution northward and offshore (Figure 2). Our observations suggest that fishing effort concentrated in the Southern California Bight during spring and shifted northward and offshore as the season progressed. In fall, fishing effort shifted southward to target swordfish. In spite of these general trends, there were also skippers who always fished the Southern California Bight and did not change their area of fishing operations. They preferred not to fish during periods when target species moved to other areas.

In the first 5 years of the study period, total annual effort nearly doubled to a high of 11,000 sets in the 1986-87 fishing season and subsequently declined to a low of 4000 sets in the 1990-91 season (Figure 3). This decline in effort coincides with increasing regulations and laws governing this fishery.

# REGULATIONS AND LAWS PERTINENT TO THE DRIFT GILL NET FISHERY

During a 4-month period (December 1979 through March 1980), swordfish incidentally caught by drift gill net were allowed by the California Fish and Game Commission to be landed and sold. When the Commission denied a request to authorize drift gill net use for catching swordfish, legislation was passed allowing special permits for drift gill net fishing (Hanan 1984; Bedford 1987). The permits were issued to those proving previous experience, significant investment, or competency in the fishery. Permit fees ($150 for shark, $150 for swordfish) were established to fund required research, and the permittee was compelled to be onboard the vessel during fishing operations. Fish buyers were required to pay $0.01/lb privilege tax on thresher sharks and shortfin makos and to report aggregate weight and total number of swordfish received. Recreational fishermen were required to report their catch of striped marlin. The allowable incidental catch of swordfish in the drift gill net fishery was set at 25% of the number of swordfish taken by the commercial harpoon and hook-and-line fisheries in any month. A similar quota of 10% of the recreational catch was set for striped marlin caught incidentally in the drift gill net fishery.

The California Department of Fish and Game (CDFG) was directed by the Legislature to study the drift gill net shark fishery, determine the effects of the fishery on swordfish and striped marlin, set up an observer program to observe the fishing operations on vessels fishing under drift gill net and harpoon permits, and report its findings. A mandatory daily logbook system was established. Drift gill net mesh sizes were set at 8 inches or larger, twine size at #18 or larger, and net length at 6000 ft or less. Additionally, the nets could be fished only between 2 h before sunset and 2 h after sunrise.

Because regulations for the drift gill net fishery were to expire in 1982 and there was legislative interest in continuing to regulate the fishery, new legislation was enacted which allowed direct targeting of commercial fishing on swordfish during a portion of the year. Commercial landings of swordfish were not tied to the sport or commercial catch of marlin or shark as had previously been required. This legislation also established the drift gill net fishery as a limited entry fishery with a maximum of 150 permits. Because the actual number of permits exceeded 150 at that time, new entrants were not allowed into the fishery until the actual number of permits issued dropped below 150. The bill increased the minimum stretched mesh size requirement to 14 inches, required the permittee to specify the fishing vessel on which the permit would be used, and specified that each net would have a radar reflector at least 10 inches in diameter on a 6-ft pole at the net end opposite the fishing vessel.

To control the incidental catch of seals and sea lions, the same legislation established time and area closures for the early summer (1 May through 31 July) around the Channel Islands. The bill also established time and area closures between the Channel Islands and the mainland during periods of expected high use by recreational or harpoon fishermen and closed the drift gill net fishery for sharks during 1 February through 30 April. It specified that during 1 May through 15 September, incidental landings of swordfish must not exceed landings of thresher shark and shortfin mako for any permittee during any calendar month, but it allowed swordfish to be landed from 16 September through 31 January without any shark poundage landing requirement. It gave the CDFG power to evaluate and close the shark and swordfish fisheries if landings of either exceeded 1.5 million lb during any 12-month period.

In 1984, an additional 35 permits were established for taking swordfish north of Point Arguello. This legislation was passed to allow entry into the drift gill net fishery to fishermen who may have missed the earlier opportunity as the fishery developed off southern California and moved northward to central and northern California.

Legislation passed in 1985 eliminated the equal shark-swordfish landing requirement and established new time and area closures intended to reduce the bycatch of marine mammals. The closures prohibited drift gill nets within 25 nautical miles of the mainland coast from 15 December through 31 January and within 75 miles of the mainland coast from 1 June through 14 August. It set the drift gill net season to 15 August through 31 January. It established a fee of $100 to transfer the permit to a boat other than the one specified on the application. A "shark drift gill net" was defined as "a drift gill net of 14 inches or greater mesh size." The legislation allowed for a maximum of 250 fm of spare or replacement netting to be aboard the fishing vessels at any time.

In 1986, the drift gill net fishery was eliminated within 12 miles of the coast north of Point Arguello and in certain areas in the Gulf of the Farallones near the mouth of San Francisco Bay. The thresher shark fishing season was reduced to 30 days in May.

More time and area closures were added in 1987 within the Southern California Bight and net length restrictions were clarified.

In 1988, legislation required that pelvic fins be left intact on thresher sharks until after landing to enable sex determination during market sampling by the CDFG. Also swordfish could be sold only to licensed fish buyers or dealers.

The U.S. Congress passed legislation in 1988 amending the Marine Mammal Protection Act of 1972 (MMPA). The amendments required vessels owners in the drift gill net fishery, which was considered likely to have marine mammal interactions, to obtain and display Federal MMPA exemption permits, report marine mammal kills, and allow Federal observers to board and observe fishing operations.

Legislation enacted in 1989 prohibited drift gill net fishing within 75 nautical miles of the mainland from 1 May through 14 July and continued the previously enacted prohibition from 1 February through 30 April; thus, it virtually eliminated the directed thresher shark fishery in California. It also directed the CDFG to revoke permits for specified findings and allowed permit transfers between fishermen for a fee of $1000. It eliminated the requirement for drift gill net permits for taking sharks north of Point Arguello.

Also in 1989, the states of California, Oregon, and Washington enacted a tristate interjurisdictional fishery monitoring plan for thresher sharks (PSMFC 1990).

During 1990, the drift gill net permit fee was temporarily increased to $330 ($250 for a partial year), a one-time between-boat permit transfer fee of $130 was continued, and a $1500 fee to transfer permits between fishermen was established.

## BYCATCH

Observer programs were mandated for the developing drift gill net fishery in 1980 and observation begun in October of that year; thus, detailed data were gathered on incidental catches during the early years of this fishery. There were no systematic observations during the 1986-87 through 1989-90 fishing seasons, after which the National Marine Fisheries Service (NMFS) established an observer program as mandated by the MMPA. Data were recorded by observers onboard or nearby the drift gill net vessels during observed net pulls. Observers recorded detailed fishing information including number of each species in the catch.

During the first 6 years of the fishery, the CDFG had two observer programs. The first observed 262 net pulls during the 1980-81, 1981-82, and 1982-83 fishing seasons. These observations were made by observers who boarded drift gill net vessels prior to leaving the fishing port and stayed aboard until the vessel returned to port. The second program observed 181 net pulls during the 1983-84, 1984-85, and 1985-86 fishing seasons. These observations were made by observers transferred to the drift gill net vessels from a CDFG vessel at the fishing grounds just prior to the net pull and transferred back to the CDFG vessel after completion of the net pull. This method of obtaining observations allowed more random selection of drift gill net vessels than the previous program, since any vessel on the fishing grounds could be boarded and observed during a net pull without regard for living space—a major consideration in selecting vessels to observe during the first observation program.

The NMFS established a mandatory drift gill net observer program during the 1990-91 fishing season and observed 195 net pulls using a sampling scheme similar to the first CDFG program. The program differed by requiring vessels to take observers on a preset proportion of the fishing trips (Lennert et al. 1991).

Observers recorded bycatch by taxon for fish, mammals, and turtles (Table 2). The potential catch of striped marlin was of particular concern to all involved in this fishery, since striped marlin were designated a sport fish in California and were not to be sold even if caught incidentally in commercial fisheries. Drift gill net fishermen were required to notify the CDFG when marlin were caught and to surrender them to the CDFG upon docking. The bycatch of striped marlin was closely monitored while the CDFG observer program was in existence. During that period, the striped marlin bycatch (Table 3) was not considered large enough to warrant additional closures or further restrictions of the fishery (Bedford 1985).

Pinnipeds and turtles, as well as small and large cetaceans, were observed caught in the drift gill net fishery (Table 3), although large cetaceans tended to break through the nets or to break free after entangling. Observations of marine mammals caught incidentally to the fishing operations (Diamond et al. 1986, 1987) were used with estimates of fishing effort to calculate total marine mammal mortalities by time and area in the fishery (Hanan et al. 1988; Herrick and Hanan 1988; Hanan and Diamond 1989; Lennert et al. 1991; Perkins et al. 1991, 1992). There were no major changes in the rates of entanglement during the period examined except for a decrease in the catch rate of pinnipeds near the Channel Islands after the implementation of time and area closures. Part of the rationale for a fishing closure within 25 miles of shore was to protect gray whales *Eschrichtius robustus*, although there were no observations of gray whales killed in the drift gill net fishery and apparently no significant effect on the population (Heyning and Lewis 1990). Heyning and Lewis (1990) also state that the entanglement of balaenopterid whales may be substantial in this fishery. Miller et al. (1983) estimated, based on dock-side interviews of fishermen, that three gray whales and one large baleen whale were killed in this fishery in 1980.

Two species of sea turtles, Ridley's *Lepidochelys olivacea* and loggerhead *Caretta*, were observed caught in the drift gill net fishery (Diamond et al. 1986, 1987). All turtles caught appeared to be dead when removed from the nets.

As mentioned above, some of the incidental catch (e.g. swordfish and opahs) became important and were even targeted as the fishery evolved. Basically, the fishermen kept what could be sold and released or discarded that which could not be sold (e.g. blue sharks, molas, and marine mammals).

TABLE 2. Target and bycatch species taken in the Calfornia drift gill net fisheries during the 1981-82 through 1990-91 fishing seasons, compiled from landing receipts and observer logs.

| Common name | Scientific name |
|---|---|
| Sharks and rays | |
| Angel shark, Pacific | *Squatina californica* |
| Basking shark | *Cetorhinus maximus* |
| Bat ray | *Myliobatis californica* |
| Blacktip shark | *Carcharhinus limbatus* |
| Blue shark | *Prionace glauca* |
| Bull shark | *Carcharhinus leucas* |
| Cow shark (unspecified) | Hexanchidae |
| Dogfish, spiny | *Squalus acanthias* |
| Dusky shark | *Carcharhinus obscurus* |
| Electric ray, Pacific | *Torpedo californica* |
| Hammerhead shark (unspecified) | *Sphyrna* spp. |
| Leopard shark | *Triakis semifasciata* |
| Mako, shortfin | *Isurus oxyrinchus* |
| Manta | *Manta birostris* |
| Megamouth shark | *Megachasma pelagios* |
| Salmon shark | *Lamna ditropis* |
| Sevengill shark | *Notorynchus cepedianus* |
| Smoothhound, brown | *Mustelus henlei* |
| Smoothhound, gray | *Mustelus californicus* |
| Soupfin shark | *Galeorhinus zyopterus* |
| Stingray, pelagic | *Dasyatis violacea* |
| Thresher, bigeye | *Alopias superciliosus* |
| Thresher, common | *Alopias vulpinus* |
| Thresher, pelagic | *Alopius pelagicus* |
| White shark | *Carcharodon carcharias* |
| Shark (unspecified) | |
| Other fishes | |
| Albacore | *Thunnus alalunga* |
| Anchovy, northern | *Engraulis mordax* |
| Barracuda, California | *Sphyraena argentea* |
| Bass, kelp | *Paralabrax clathratus* |
| Bonito, Pacific | *Sarda chiliensis* |
| Butterfish, Pacific | *Peprilus simillimus* |
| Dolphinfish (Mahi mahi) | *Coryphaena hippurus* |
| Hake, Pacific | *Merluccius productus* |
| Louvar | *Luvarus imperialis* |
| Mackerel, bullet | *Auxis rochei* |
| Mackerel, jack | *Trachurus symetricus* |
| Mackerel, Pacific | *Scomber japonicus* |

TABLE 2. (continued)

| Common name | Scientific name |
|---|---|
| Other fishes (continued) | |
| Marlin, black | *Makaira indica* |
| Marlin, striped | *Tetrapturus audax* |
| Mola (Ocean sunfish) | *Mola mola* |
| Needlefish, California | *Strongylura exilis* |
| Opah | *Lampris guttatus* |
| Pipefish (unspecified) | Syngnathidae |
| Remora (unspecified) | Echeneidae |
| Salmon (unspecified) | *Oncorhynchus* spp. |
| Sardine, Pacific | *Sardinops sagax* |
| Seabass, white | *Atractoscion nobilis* |
| Sheephead, California | *Semicossyphus pulcher* |
| Skipjack, black | *Euthynnus lineatus* |
| Swordfish | *Xiphias gladius* |
| Tuna, bigeye | *Thunnus obesus* |
| Tuna, bluefin | *Thunnus thynnus* |
| Tuna, skipjack | *Katsuwonus pelamis* |
| Tuna, yellowfin | *Thunnus albacares* |
| Whitefish, ocean | *Caulolatilus princeps* |
| Wahoo | *Acanthocybium solandri* |
| Yellowtail | *Seriola lalandi* |
| Marine mammals | |
| Beaked whale (mesoplodont) | *Mesoplodon* spp. |
| Common dolphin | *Delphinus delphis* |
| Dall's porpoise | *Phocoenoides dalli* |
| Elephant seal, northern | *Mirounga angustirostris* |
| Finback whale | *Balaenoptera physalus* |
| Gray whale, California | *Eschrichtius robustus* |
| Harbor seal, Pacific | *Phoca vitulina* |
| Minke whale | *Balaenoptera acutorostrata* |
| Pilot whale, short-finned | *Globicephala macrorhynchus* |
| Right whale dolphin, northern | *Lissodelphis borealis* |
| Risso's dolphin | *Grampus griseus* |
| Sea lion, California | *Zalophus californianus* |
| White-sided dolphin, Pacific | *Lagenorhynchus obliquidens* |
| Turtles | |
| Loggerhead | *Caretta caretta* |
| Ridley's | *Lepidochelys olivacea* |

TABLE 3. Observed bycatch rates (individuals per net) of striped marlin, marine mammals, and turtles in the California drift gill net fishery during the 1980-81 through 1984-85 and 1990-91 seasons. Observations for the 1980-81 through 1982-83 seasons are combined as they represent the first sampling method used by the CDFG. The 1990-91 data were collected by the NMFS.

| | 1980-83[a] | 1983-84 | 1984-85 | 1985-86 | 1990-91 |
|---|---|---|---|---|---|
| Number of observations | 226 | 71 | 44 | 66 | 195 |
| Striped marlin | 0.048 | 0.085 | 0.068 | 0.061 | 0.067 |
| Marine mammals | | | | | |
| California sea lion | 0.364 | 0.085 | 0.023 | 0.015 | 0.026 |
| Northern elephant seal | - | 0.028 | - | 0.030 | 0.021 |
| Pacific harbor seal | - | - | - | 0.015 | 0.005 |
| Common dolphin | - | - | 0.068 | 0.106 | 0.077 |
| Dall's porpoise | - | - | - | - | 0.010 |
| Northern right whale dolphin | - | - | - | 0.015 | 0.005 |
| Pacific white-sided dolphin | 0.004 | - | - | - | 0.015 |
| Risso's dolphin | - | - | - | - | 0.010 |
| Baleen whale (unspecified) | 0.009 | - | - | - | - |
| Finback whale | 0.004 | - | - | - | - |
| Gray whale | 0.004[b] | - | - | - | - |
| Mesoplodont beaked whale | - | - | - | 0.030 | 0.005 |
| Minke whale | - | - | 0.023 | 0.015 | - |
| Short-finned pilot whale | 0.009 | - | - | - | 0.005 |
| Turtles | | | | | |
| Loggerhead | - | 0.014 | - | - | - |
| Ridley's | - | 0.014 | - | - | - |

[a] *There were 262 net pulls observed during the period October 1980 to April 1983 when the fishery was allowed year-round. Bycatch-rate data are presented for only the May through January period to allow comparison to subsequent years when the fishery was closed February through April. There was an additional closure within 75 miles of shore 1 May through 14 July 1990, but all data for the 1990-91 season are presented.*

[b] *This represents one animal, which was released alive.*

From a political viewpoint, the important species in the bycatch were gray whale, striped marlin, minke whale *Balaenoptera acutorostrata*, California sea lion, common dolphin *Delphinus delphinus*, and blue shark; from an economic viewpoint, swordfish, albacore, and opah. Species of special interest or novelty included megamouth shark *Megachasma pelagios*, basking shark *Cetorhinus maximus*, and white shark *Carcharodon carcharias*.

## STATUS OF BIOLOGICAL KNOWLEDGE

### Swordfish

Swordfish have a cosmopolitan distribution in tropical, subtropical, and temperate waters of the Pacific Ocean between lat. 50°N and 45°S and usually in water temperatures greater than 13°C (Nakamura 1985). Areas of highest apparent abundance (based on hook rates from worldwide longline fisheries) occur in waters off Australia, Mexico, Peru, Japan, and in the North Pacific Transition Zone (Sakagawa and Bell 1980). Swordfish larvae are found throughout the tropical central and western Pacific and are often associated with the 24°C surface isotherm (Nishikawa and Ueyanagi 1974).

Swordfish are both epipelagic and mesopelagic and have been reported to depths of at least 550 m. Sonic tracking experiments off southern Baja California, Mexico indicate that swordfish move from inshore areas during the day seaward to deeper areas at dusk and return to inshore areas at sunrise. Larger swordfish tend to spend more time farther offshore (Carey and Robison 1981; Carey 1990). The number of swordfish tagged in the Pacific is very low and returns have yet to confirm trans-Pacific movements. Catch records from Japanese longliners suggest a movement from the tip of Baja California in the spring northward in the summer and fall to at least the waters off California (Kume and Joseph 1969). Catch records from the California drift gill net fishery show swordfish passing through the fishery from August through January (Sakagawa 1989).

Data on length-weight relations for swordfish in the Pacific are very limited. Skillman and Yong (1974) described the relation as

$$W = 2.3296 \times 10^{-7} L^{3.5305}$$

where W = round weight (kg) and L = length from tip of upper bill to fork (cm). However, the relation is based on a sample of only seven fish between 150 and 325 cm. More length-weight data from larger samples and greater length ranges are available for swordfish in the Atlantic Ocean (Palko et al. 1981).

Most swordfish are landed dressed; a conversion factor from dressed weight to round weight was established by California Fish and Game Commission for landing-tax purposes. The regulation specifies that, for taxing, round weight be 145% of the landed weight (Calif. Code of Reg., Title 14, section 187).

There is good evidence that male and female swordfish grow at different rates with females attaining the larger sizes (Kume and Joseph 1969). While male swordfish seldom exceed 140 kg, females may grow to 500 kg in the South Pacific. Swordfish in the western Pacific grow approximately 25 to 30 cm/year, whereas swordfish in the eastern Pacific grow approximately 38 cm/year. Approximate ages at length are as follows (Yabe et al. 1959):

| Fork length (FL) range (cm) | Age Months | Age Years |
|---|---|---|
| 38- 68 | 6-17 | 1 |
| 68- 98 | 18-29 | 2 |
| 98-128 | 30-41 | 3 |
| 128-158 | 42-53 | 4 |
| 158-189 | 54-65 | 5 |

Swordfish spawn throughout the year in warm equatorial waters, usually in close proximity to the 24°C surface isotherm (Nishikawa and Ueyanagi 1974). However, fish in spawning condition are caught more frequently during March through July in the northern latitudes and during January in the southern latitudes (Kume and Joseph 1969). There is some evidence of seasonal spawning 1 to 2 months earlier in the southwestern Pacific than around Hawaii (Matsumoto and Kazama 1974). First spawning occurs at 5 or 6 years. Fecundity is estimated at 2 to 5 million eggs per spawning in the western Pacific (Nakamura 1985).

Larval swordfish, 9.0 to 14.0 mm total length (TL), feed on organisms such as mysids and amphipods, and start feeding on fish at about 21 cm (Yabe et al. 1959). Juveniles and larger swordfish are opportunistic feeders concentrating on areas of high food abundance. They feed on local species of squid, fish, and pelagic crustaceans during the night (Scott and Tibbo 1968), and various bottom species while inhabiting deeper waters during the day (Nakamura 1985). The Southern California Bight provides swordfish ample prey during the summer and fall months around offshore banks and submarine escarpments.

There are no estimates of natural (*M*) or fishing (*F*) mortality rates for swordfish in the Pacific Ocean. Because of their longevity, *M* is thought to be low compared to other billfishes. Estimates of *M* for northwestern Atlantic swordfish range from 0.21 to 0.43 and estimates of total mortality rates range from 0.12 to 0.65 for the harpoon fishery and 0.16 to 0.59 for the longline fishery (Beardsley 1978).

Currently, there are two stock-structure hypotheses for Pacific swordfish (Sakagawa and Bell 1980). The first hypothesis suggests a single Pacific-wide stock in a contiguous distribution with zones of high catches, high abundance, and the assumption that the population is sufficiently mobile within its range to prevent local depletion. The second hypothesis emphasizes three stocks in areas of high abundance made contiguous over a broad area of low abundance. In both cases, stock assessments conclude that Pacific swordfish populations are not overfished and that the resource is healthy (Bartoo and Coan 1989) and being fished at levels much lower than in the mid-1960s.

## Thresher Sharks

Three species of thresher sharks are taken in California's drift gill net fishery: common thresher, bigeye thresher, and pelagic thresher. Although all three are closely related and share many common traits, they are caught at vastly different rates in this fishery.

### *Common Thresher*

Common threshers are distributed throughout all tropical and temperate oceans. They are both coastal and oceanic but have a greater apparent abundance within 40 miles of shore (Strasburg 1958). They are strong swimmers, although transoceanic migrations are undocumented in the Pacific. In the eastern North Pacific they are abundant over the continental and insular shelves (Compagno 1984a), distributed seasonally from Baja California to Vancouver Island, British Columbia.

Common threshers move northward from Baja California into southern California following the warmwater isotherms in early spring. Large mature common threshers continue northward to at least Vancouver Island in late summer and fall, where the sex ratio can be five males per female (Stick and Hreha 1988, 1989). Presumably there is a southward movement in winter. Juveniles tend to remain in shallow, nearshore areas especially within the Southern California Bight, which may be an important nursery area (Bedford 1992). Immature fish are seldom found north of Cape Mendocino, California (Holts and Bedford 1989).

The caudal fin or tail of thresher sharks represents about 50% of total body length. Minimum size at birth was estimated at 139 cm TL, while maximum total length, based on a sample of 143 common threshers taken off California, was estimated at 636 cm for females and 493 cm for males (Cailliet and Bedford 1983). Maximum age was also estimated to be as high as 45 to 50 years (Cailliet et al. 1983).

The relation between alternate length (AL, distance from origin of first dorsal fin to origin of second dorsal fin) and dressed weight was determined for 110 common threshers (combined sexes) sampled at Washington and Oregon ports (Stick and Hreha 1988). That relation was

$$W = 0.001305(AL)^{2.750031}$$

were W = dressed weight (lb) and AL = alternate length (cm). There are no data relating dressed to round weight for common threshers. The California Fish and Game Commission established regulations for determining landing taxes which specify a 170% factor of the landed weight to be the round weight for taxing purposes.

Reproduction in common threshers is ovoviviparous. After absorption of the yolk sac, developing fetuses obtain nourishment by eating eggs still developing in the uterus (Bigelow and Schroeder 1948; Otake and Mizue 1981). Females mature at 315 cm TL in the Pacific (Strasburg 1958) and males reach maturity at about 333 cm TL (Cailliet and Bedford 1983). Mating occurs in summer. Gestation lasts 9 months and female common threshers give birth each spring (March to June) to an average of four fully developed pups (Bedford 1985).

Thresher sharks use their tail to thrash and stun their prey. In the eastern North Pacific, their diet consists of small pelagic species including anchovies, herring, mackerel, sardines, and squid (Hart 1973; Stick and Hreha 1989).

Due to their long life and the advanced stage and condition of newborn pups, natural mortality is presumed low. There has been one attempt at estimating fishing mortality for the eastern Pacific common thresher. Hanan (1984) suggested sustainable mortality rates for a closed fishery, although preliminary, were very low ($F = 0.007$ to 0.049), implying that only a small portion of the stock could be removed annually without compromising the stock.

Separate oceanic stocks may exist; differences have been observed in numbers of offspring and size at maturity in the Indian Ocean (Gubanov 1972) and in the North Pacific (Strasburg 1958; Cailliet and Bedford 1983). Fishery data suggest that the common thresher resource off California consists of a single, coast-wide stock. This stock appears to have a seasonal north-south movement pattern. Numerous thresher sharks taken off the California coast have carried hooks from the Japanese billfish and tuna longline fishery indicating long-distance movement from southern or offshore areas (Bedford 1985). However, the declining catch and smaller size of individuals in the catch indicate immigration has not kept pace with the harvest rates predicted by Hanan (1984). A preliminary population assessment for the 1980-84 period, using catch per unit effort and cohort analysis, indicated that the local stock could not sustain the level of catch evaluated in that 4-year period of study (Berkson 1985). More complete or rigorous stock assessments have not been conducted. During the period and area of this study, fishery data showed that catches of common thresher decreased and the average size remained small in spite of the numerous regulations restricting fishing effort (Cailliet et al. in press).

## *Pelagic Thresher*

Pelagic threshers are found in tropical Pacific and Indian Ocean waters. They are oceanic and epipelagic and occasionally found near inshore areas. Little is known concerning their movements off the coasts of California and Mexico.

They are smaller than other thresher sharks and grow from 96 cm at birth to 330 cm maximum length (Compagno 1984a). Reproduction is ovoviviparous with two pups per litter. Size at maturity is not well documented but is between 264 and 282 cm TL (Otake and Mizue 1981; Compagno 1984a).

There is no information on mortality rates or stock status in the Pacific. Evidence from the longline fishery suggests a population center off central Baja California which shifts northward during strong El Niño events.

## *Bigeye Thresher*

Bigeye threshers, like common threshers, are oceanic and coastal in tropical, sub-tropical, and warmer temperate seas. They are epipelagic and have been reported to depths of at least 500 m (Compagno 1984a). In the eastern North Pacific they are found on the high seas, over continental and insular shelves, and occasionally in shallow inshore areas. The first report of this species from southern California waters was of a 1963 occurrence of a bigeye thresher caught in a set gill net (Fitch and Craig 1964).

Maximum reported size is 461 cm TL for females and 378 cm TL for males. Size at birth is between 64 and 106 cm TL (Gruber and Compagno 1981). The length-weight relation reported for 16 Atlantic bigeye threshers by Stillwell and Casey (1976) is

$$\text{Log } Y \text{ (WT)} = 11.1204 + 2.99269 \text{ Log } X \text{ (FL)}$$

where WT = weight (kg) and FL = fork length (cm).

Reproduction is ovoviviparous as in other thresher sharks. Males mature at about 300 cm TL (3 to 4 years) while females become sexually mature at about 350 cm TL (5 to 6 years old; Gruber and Compagno 1981).

Bigeye threshers have specialized eyes adapted to low light levels. Their eyes can roll up into upward-directed sockets allowing them to feed on prey species silhouetted above. Their prey consists of small pelagic fish, squid, and crustaceans (Stillwell and Casey 1976; Gruber and Compagno 1981).

Although fished throughout its range, very little is known about mortality rates, stock structure, or stock status. The species is widely, though sparsely, distributed and may commonly inhabit deep water (Gruber and Compagno 1981).

## Shortfin Mako

Shortfin makos are found in all tropical and warmer temperate oceans and in both coastal and open-ocean habitats. In the extreme northern and southern portions of their range, they follow warm water masses poleward in summers. They are highly migratory and considered one of the fastest and most active ocean predators (Compagno 1984a). General movement patterns or centers of abundance in the eastern North Pacific are not well known (Strasburg 1958). Juveniles are generally caught more frequently in the waters off southern California in the summer months and seldom caught north of the Mendocino Escarpment. Juveniles are near-surface swimmers and rarely descend below the thermocline (Holts and Bedford in press). Adults are occasionally caught around the Channel Islands and outer banks of the Southern California Bight in late summer.

Maximum total length reported is 390 cm for females and 280 cm for males. The largest shortfin mako reported off California was 351 cm and weighed 468 kg (Applegate 1976). Cailliet et al. (1983) estimated von Bertalanffy asymptotic growth from 44 southern California shortfin makos (combined sexes) at $L_\infty =$ 321 cm TL, with an estimated life span of 45 years. Pratt and Casey (1983), assuming two vertebral growth bands per year, determined asymptotic growth from 109 Atlantic shortfin makos at $L_\infty =$ 345 cm FL for females and 302 cm FL for males. Strasburg (1958) described the length-weight relation as

$$\log \mathrm{WT\ (lb)} = -4.608 + 2.925 \times \mathrm{TL\ (cm)}$$

for central Pacific shortfin makos, and Stevens (1983) reported

$$\mathrm{WT\ (kg)} = 4.582 \times 10^{-6}\ \mathrm{TL}^{3.10}\ \mathrm{(cm)}$$

from 80 shortfin makos taken off New South Wales.

Reproduction is ovoviviparous with 4 to 16 pups per litter. Gestation is about 1 year with parturition occurring in late spring followed by mating in the summer months. Females mature at 280 cm TL (7 to 8 years) and males mature at 195 cm TL. Mean size at birth is 70 cm TL (Stevens 1983).

Shortfin makos are active feeders on a variety of epipelagic species (Stillwell and Kohler 1982). Off California these include mackerel, bonito, anchovy, tuna, other sharks, and squid. They are even known to kill and eat swordfish (Bigelow and Schroeder 1948).

There are no estimates of natural or fishing mortality rates for the shortfin mako. Stock structure and abundance of shortfin makos in the eastern Pacific are poorly understood. Length-frequency and catch data from the drift gill net fishery suggest that southern California waters are part of an important nursery area for shortfin makos in the eastern Pacific.

## Blue Shark

Blue sharks are circumglobal in all tropical and temperate waters. In the North Pacific, seasonal migrations occur between lat. 20° and 50°N. They are epipelagic and generally considered abundant in the offshore and coastal waters of the western United States and Mexico (Compagno 1984b). The northward movement extends into the Gulf of Alaska as waters warm during summer months. Movement southward occurs during winter months (Strasburg 1958). In coastal areas, mature females tend to start their northward journey in early spring as warm water moves northward, while juveniles of both sexes follow closely. Large males start later and tend to stay farther offshore (Bedford 1985). Juveniles and subadults are abundant within the Southern California Bight and in Monterey Bay from May to October (Sciarrotta and Nelson 1977; Tricas 1979).

Cailliet and Bedford (1983) determined asymptotic growth ($L_\infty$) from 130 southern California blue sharks at 242 cm TL for females and 295 cm TL for males. Length-weight relations for Pacific blue shark were described by Nakano et al. (1985) as

$$WT = 3.838 \times 10^{-6} \ L^{3.174} \text{ for males}$$

$$WT = 2.328 \times 10^{-6} \ L^{3.294} \text{ for females}$$

where WT = weight (kg) and L = precaudal length (cm). Strasburg (1958) reported

$$\log WT = -5.396 + 3.13439(\log TL) \text{ for combined sexes}$$

where WT = weight (lb) and TL = total length (cm).

Blue sharks are viviparous, thus developing embryos are initially nourished from a yolk sac. Once the yolk sac is exhausted, developing young obtain nourishment and oxygen from the maternal blood stream through a placenta. Females mature at 140 to 160 cm FL (5 to 6 years) and males mature a year earlier between 130 and 160 cm FL (Nakano 1991). Maximum age is estimated to be at least 20 years (Cailliet and Bedford 1983; Nakano 1991). Gestation is 9 to 12 months. Brood size varies considerably depending on the female's size and condition, with over 100 young in a single brood reported, although 20 to 40 young are more typical (Strasburg 1958). Nakano (1991) examined 669 pregnant females from the North Pacific and found a mean litter size of 25.6 pups with an overall sex ratio of 1:1. Off California, parturition occurs in early spring and mating occurs during late spring to early winter. The Southern California Bight is a major pupping area and generally considered a nursery area for immature blue sharks. They are often seen on calm days moving slowly with dorsal fin and tail lobe protruding from the water.

In the coastal waters off California, blue sharks feed on anchovy, mackerel, hake, dogfish, squid, and pelagic crustaceans (Tricas 1979; Harvey 1989). Juveniles may make shoreward movements at night to feed in shallow water especially in the Southern California Bight, where numerous islands and submerged banks attract ample prey (Sciarrotta and Nelson 1977).

The size of the blue shark stock subject to the drift gill net fishery is unknown. There are no local or Pacific-wide estimates of stocks or abundance. Local availability undergoes major seasonal fluctuations with more juveniles (1 to 3 years old) caught in the coastal waters from early spring to early winter. Mature adults are uncommon in coastal waters. Local abundance probably depends on recruitment from coastal Mexican and offshore areas. A blue shark tagged off southern California was recovered near Midway Island in the central Pacific (J.S. Sunada, CDFG, pers. comm.), suggesting that it is a cosmopolitan species and that the local stock is not a closed population.

Fishery-dependent and -independent data needed for determining abundance, mortality, and distribution are inadequate. Blue sharks caught incidentally are usually discarded because the meat is considered unsuitable for human consumption; thus this catch often goes undocumented and little biological data are gathered.

### Opah

Opahs are found in all tropical and temperate oceans. In the eastern North Pacific they are caught in the drift gill net fishery for swordfish, by trollers from the Gulf of California to the Gulf of Alaska (Hart 1973), and as incidental catches in other fisheries operating off southern California. They are rarely caught in large numbers and are thought to be widely but sparsely distributed (Allen 1992). General movement patterns are unknown, although opahs occur in the waters off California at all times of the year to depths of 365 m (Harald 1939). These fish may reach 180 cm and exceed 225 to 275 kg in the Atlantic. The largest reported off California was 73 kg (Harald 1939).

Opah feed on crustaceans, cephalopods, and small boney fishes (Allen 1992). There is little information on growth, reproduction, stock size, or status of the opah stock. They are apparently more abundant off California following El Niño years. Because opah is not a target species in any fishery, current landings probably have little impact on the population as a whole (Allen 1992).

### Tuna

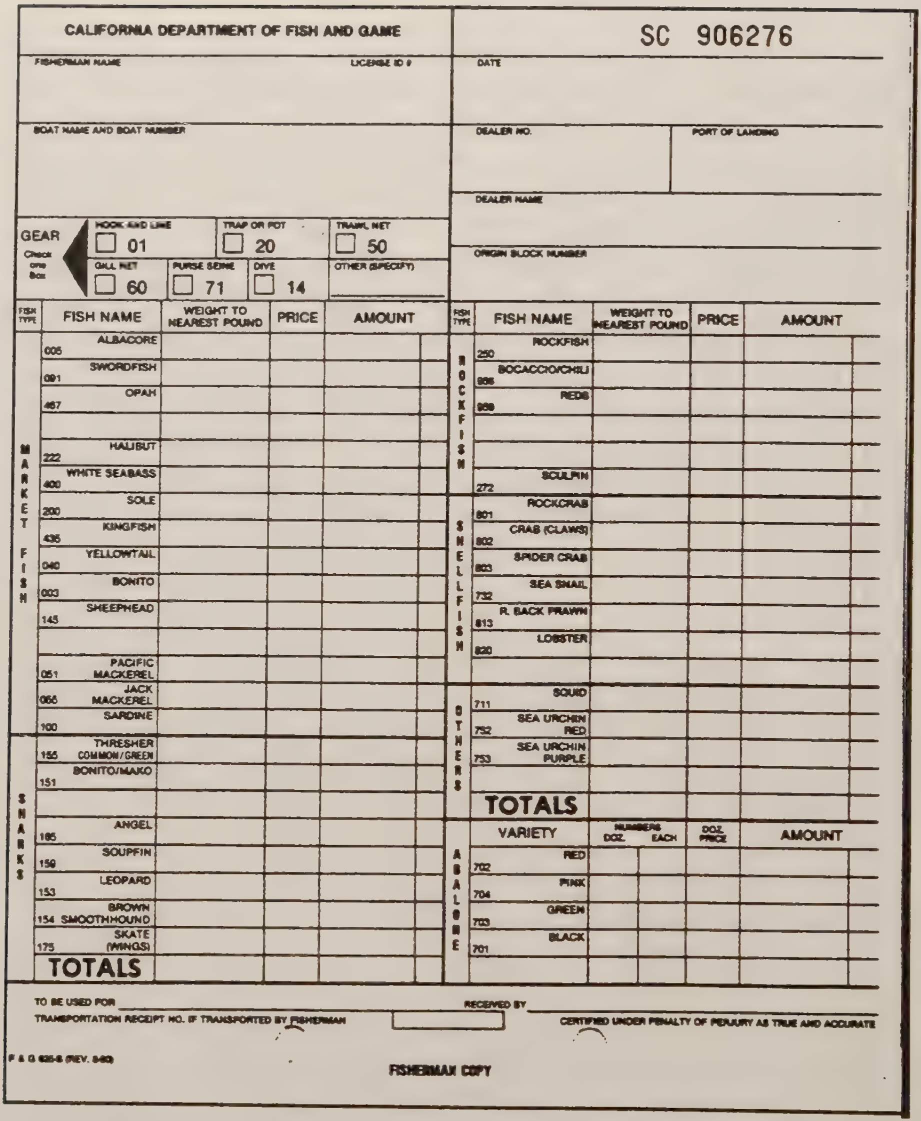
The California drift gill net fishery occasionally catches albacore, skipjack, bigeye, and yellowfin tunas. The status of biological knowledge, stock status, and summaries of directed fisheries for those species can be found in Bartoo (1987), Bayliff (1992), Laurs and Dotson (1992), and Wild (1992).

## CATCH ANALYSIS

### Landings

Commercial fish buyers have been required to complete a landing receipt (Figure 7) for each landing purchased in California since the early 1900s. The buyer recorded species landed, quantity landed (pounds), price, and fishing gear used (Bureau of Marine Fisheries 1952). Other data such as area fished could have been reported on the landing receipts but often these sections were left blank.

While the instructions for the landing receipts asked buyers to report gill net landings by type of gill net (drift or set), the receipts have an entry only for generic gill net (coded as entangling net in the data base). Because of this ambiguity on the receipt, fish buyers at times neglected to identify the type of gill net used. Also, swordfish, thresher sharks, and shortfin makos, species typically caught by drift gill net, were sometimes reported taken by gear such as trawls, trammel nets, and encircling net—gear that does not ordinarily catch these species. Be-



**CALIFORNIA DEPARTMENT OF FISH AND GAME**

SC 906276

FISHERMAN NAME

LICENSE ID #

DATE

BOAT NAME AND BOAT NUMBER

DEALER NO.

PORT OF LANDING

DEALER NAME

ORIGIN BLOCK NUMBER

GEAR Check one Box

| | | | |
|---|---|---|---|
| HOOK AND LINE ☐ 01 | | TRAP OR POT ☐ 20 | TRAWL NET ☐ 50 |
| GILL NET ☐ 60 | PURSE SEINE ☐ 71 | DIVE ☐ 14 | OTHER (SPECIFY) |

| FISH TYPE | FISH NAME | WEIGHT TO NEAREST POUND | PRICE | AMOUNT |
|---|---|---|---|---|
| MARKET FISH | 005 ALBACORE | | | |
| | 091 SWORDFISH | | | |
| | 467 OPAH | | | |
| | | | | |
| | 222 HALIBUT | | | |
| | 400 WHITE SEABASS | | | |
| | 200 SOLE | | | |
| | 435 KINGFISH | | | |
| | 040 YELLOWTAIL | | | |
| | 003 BONITO | | | |
| | 145 SHEEPHEAD | | | |
| | | | | |
| | 051 PACIFIC MACKEREL | | | |
| | 066 JACK MACKEREL | | | |
| | 100 SARDINE | | | |
| SHARKS | 155 THRESHER COMMON/GREEN | | | |
| | 151 BONITO/MAKO | | | |
| | | | | |
| | 165 ANGEL | | | |
| | 159 SOUPFIN | | | |
| | 153 LEOPARD | | | |
| | 154 BROWN SMOOTHHOUND | | | |
| | 175 SKATE (WINGS) | | | |
| | **TOTALS** | | | |

| FISH TYPE | FISH NAME | WEIGHT TO NEAREST POUND | PRICE | AMOUNT |
|---|---|---|---|---|
| ROCKFISH | 250 ROCKFISH | | | |
| | 956 BOCACCIO/CHILI | | | |
| | 959 REDS | | | |
| | | | | |
| | | | | |
| | 272 SCULPIN | | | |
| SHELLFISH | 801 ROCKCRAB | | | |
| | 802 CRAB (CLAWS) | | | |
| | 803 SPIDER CRAB | | | |
| | 732 SEA SNAIL | | | |
| | 813 R. BACK PRAWN | | | |
| | 820 LOBSTER | | | |
| | | | | |
| OTHERS | 711 SQUID | | | |
| | 752 SEA URCHIN RED | | | |
| | 753 SEA URCHIN PURPLE | | | |
| | | | | |
| | **TOTALS** | | | |

| | VARIETY | NUMBERS DOZ. | NUMBERS EACH | DOZ. PRICE | AMOUNT |
|---|---|---|---|---|---|
| ABALONE | 702 RED | | | | |
| | 704 PINK | | | | |
| | 703 GREEN | | | | |
| | 701 BLACK | | | | |
| | | | | | |

TO BE USED FOR ____________________

TRANSPORTATION RECEIPT NO. IF TRANSPORTED BY FISHERMAN ☐

RECEIVED BY ____________________

CERTIFIED UNDER PENALTY OF PERJURY AS TRUE AND ACCURATE

F & G 625-B (REV. 8-83)

FISHERMAN COPY

FIGURE 7. Current landing receipt used by commercial buyers of fish landed by the California drift gill net fishery.

cause of these problems associated with reported gear types, criteria were developed to estimate actual landings of the drift gill net fishery.

Landing receipts were separated into three categories: 1) landings with gear reported as drift gill net, 2) landings by vessels with drift gill net-permitted skippers but with gear reported as other than drift gill net, and 3) landings with gear reported as entangling net, trawl, trammel net, encircling net, or set gill net. All landings in category 1 were assumed correct and summed directly as drift gill net landings. (This included the landings for a relatively small number of vessels using drift gill nets and targeting species such as California barracuda, white seabass, and yellowtail *Seriola lalandi*. These vessels fish nearshore waters and use nets with 6-inch or smaller mesh. Their landings are included in Tables 1 and 2.)

Criteria for identifying and separating drift gill net landings from categories 2 and 3 were based on category 1 landings for the 1981-82 and 1982-83 seasons, the period with the fewest reports of catch by unspecified net type (no net type reported in the landing receipt gear code section). Landings for this period were summarized to determine the relative proportions of fish species for both drift and set gill nets. Typically, drift gill net landings had catch proportions of swordfish greater than 20%, thresher shark greater than 30%, and shortfin mako greater than 18%; whereas landings from set gill nets had catch proportions of swordfish less than 6%, thresher shark less than 8%, and shortfin mako less than 2%. Relatively large percentages of Pacific herring *Clupea pallasi* (greater than 70%) were identified as set gill nets. Also noted in set net landings were angel shark, rays, and skates; these nearshore species were rarely reported in drift gill net landings.

Based on the above findings, category 2 and 3 landings were considered drift gill net landings if no Pacific herring was landed and if landings receipts reported gear as entangling nets, trammel nets, trawls, encircling nets, or set gill nets and the landing contained more than 20% swordfish, 30% thresher shark, or 18% shortfin mako. Landings were not included in the drift gill net summaries if angel sharks, rays, skates, or California sheephead *Semicossyphus pulcher* were reported.

Landings in category 2 were screened with additional criteria if the reported gear was "unknown." These landings were considered drift gill net landings if 1) swordfish was greater than 20% and thresher shark greater than 30% of the fish landed, or 2) swordfish landed was greater than 20% and shortfin mako was greater than 18%, or 3) thresher shark was greater than 30% and shortfin mako was greater than 18%. These criteria were developed to insure that "gear unknown" landings reported as 100% swordfish would not be included as gill net landings, but more appropriately as harpoon landings.

Data summarized with the above criteria show that the number of drift gill net vessel landings increased to a high of 3500 in the 1983-84 season and decreased steadily to a low of 1500 in the 1990-91 season (Figure 8a). The number of drift gill net vessels peaked in 1985-86 at 309 and decreased to less than 200 in the 1990-91 season (Figure 8b). The number of vessels shown in Figure 8b are at times higher than the annual 250-vessel permit limit. This was caused by the criteria used to estimate drift gill net fishery landings, where some landings with

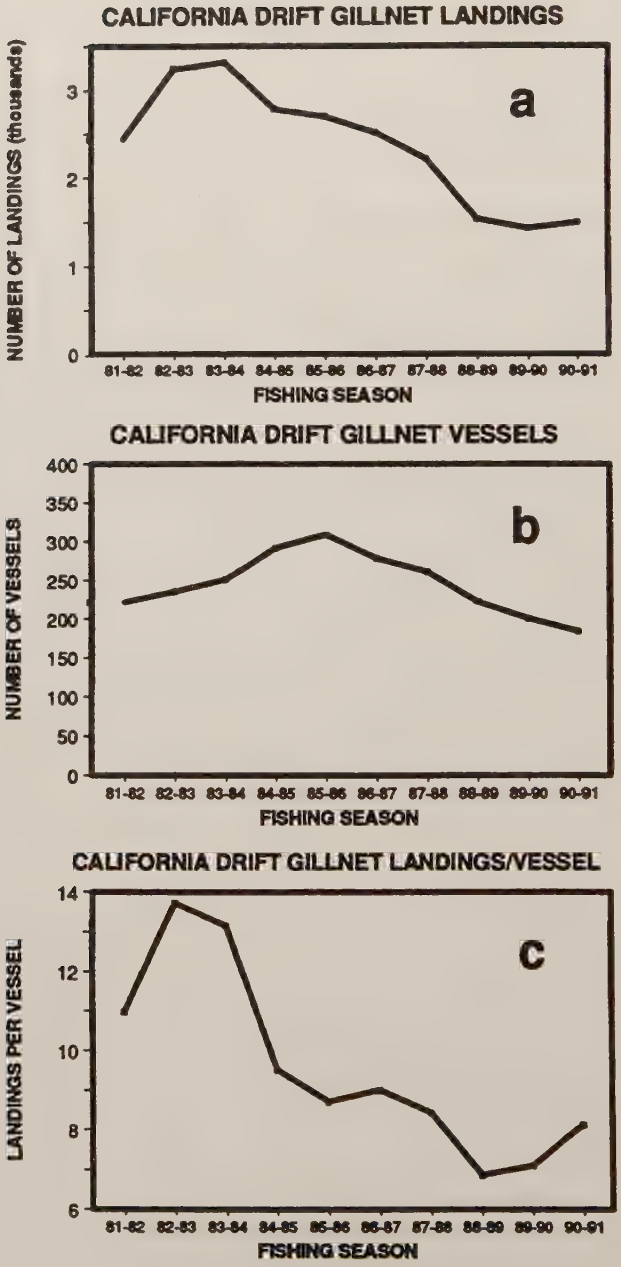


FIGURE 8. Number of landings (a), vessels (b), and landings per vessel (c) for the California drift gill net fishery, 1981-82 through 1990-91.

gear identified as drift gill net were made by a nonpermitted vessel. Landings per vessel decreased sharply from a high of 13 in the 1982-83 season to lows of seven and eight in the 1988-89 to 1990-91 seasons (Figure 8c).

The principle species landed by the drift gill net fishery were swordfish, common thresher, and shortfin mako (Table 1). Common thresher dominated the catch in the 1981-82 (60%) and 1982-83 (48%) fishing seasons, but swordfish dominated during the 1983-84 to 1990-91 (53% to 68%) fishing seasons (Figure 9). Swordfish landings increased from a low of 700,000 lb in the 1981-82 season to a high of 3.4 million lb in the 1984-85 season and then declined to 1.5 million lb in the 1990-91 season. Common thresher landings decreased steadily from a high of 2.2 million lb in the 1981-82 season to a relatively constant level of 400,000 to 500,000 lb during the 1986-87 to 1990-91 seasons. Landings of shortfin mako peaked in the 1982-83 season at 500,000 lb, but have remained relatively stable between 200,000 and 300,000 lb since then.

Other species were also landed in the drift gill net fishery, although in lesser quantities (Table 1). The largest quantity in this group was tuna, dominated by albacore which peaked at over 200,000 lb in the 1985-86 season and dwindled to 23,000 lb in the 1990-91 season. Shark landings other than thresher and shortfin mako were dominated by the "unspecified shark" category during the early seasons and by soupfin shark during the later seasons. The recorded high landings of over 200,000 lb of "unspecified shark" in the 1981-82 season may include a high rate of accidental or intentional misidentification of illegally caught and landed swordfish. Opah dominated catches of other fish species and reached a high of 260,000 lb in the 1984-85 season.

## Logbooks

Logbooks have been collected from skippers of California drift gill net vessels under a mandatory logbook system implemented in 1980 (Huppert and Odemar 1986). Data collected from the logbooks include catches (number of fish) by species, date, mesh size, length of net, hours soaked, set number, geographical position of set, and other information such as the drift gill net permit number and vessel registration number (Figure 10).

Geographical positions entered on logbooks were CDFG block numbers (usually a 10-min square). We converted these block numbers to latitude and longitude for plotting. Some catch locations were either a series of block numbers or blocks larger than a 10-min square. For those cases, a latitude and longitude for a quadrangle encompassing all of the catch locations was chosen (e.g. 1°, 5°, 5° x 10°, or larger quadrangle).

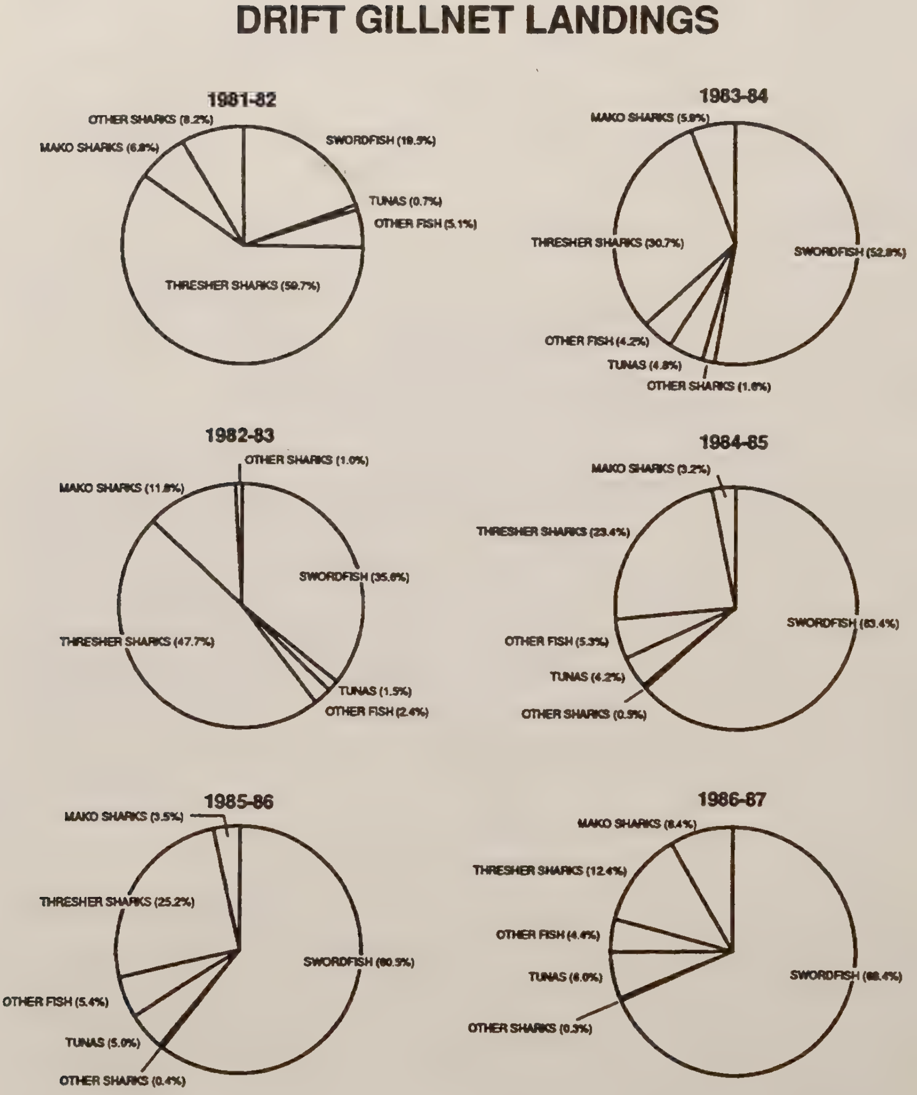


FIGURE 9a. Species composition of California drift gill net landings for the 1981-82 through 1986-87 fishing seasons.

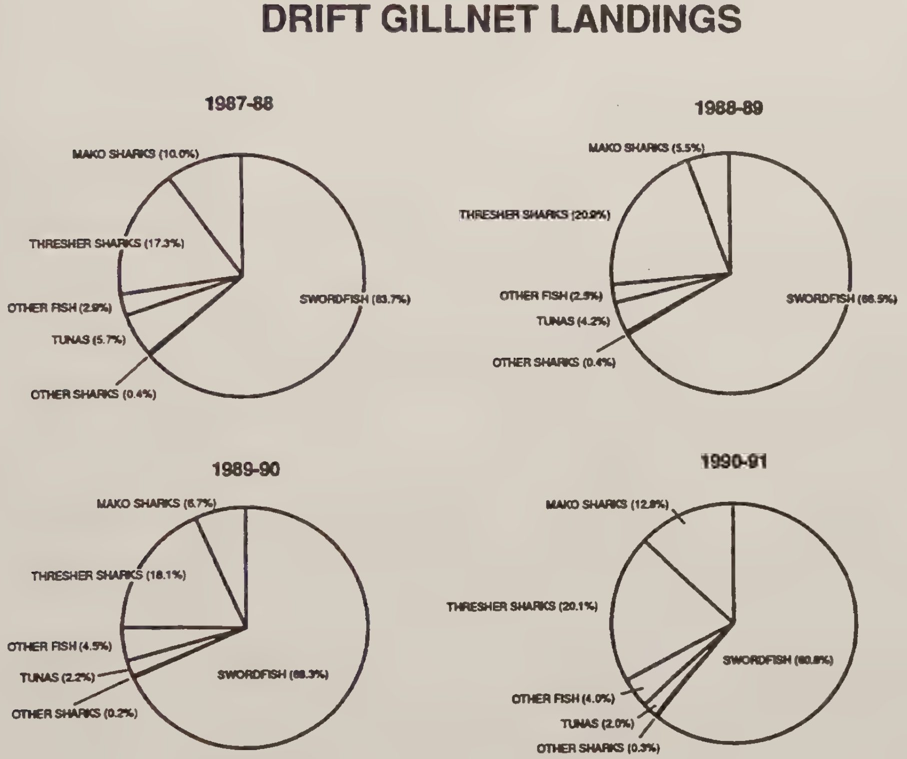
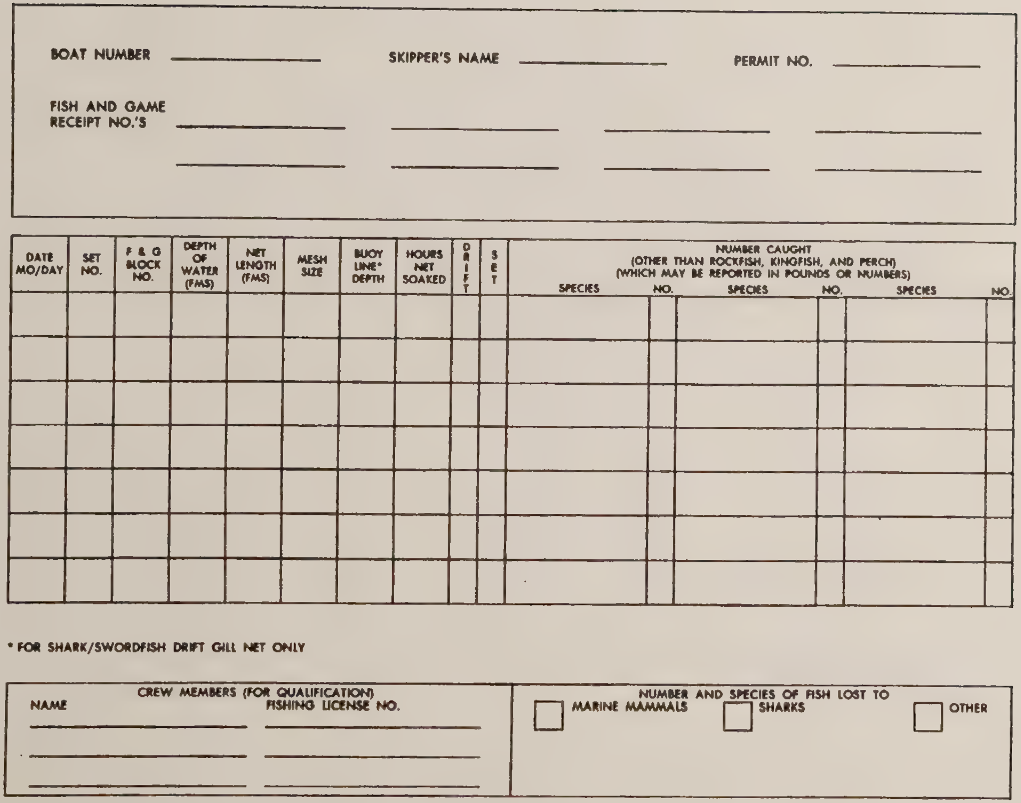


FIGURE 9b. Species composition of California drift gill net landings for the 1987-88 through 1990-91 fishing seasons.

Logbooks were collected from a majority of the drift gill net fleet and included data on most species caught, especially those that could be sold. Due to the volume of the data collected, this report will show seasonal and geographical distributions of only the four major species groups: swordfish, thresher sharks (common, pelagic, and bigeye), shortfin mako, and opah.

Coverage rates (proportion of landed fish weight reported in the logbooks) were determined by converting logbook catch to weight (number of fish times mean weight) and dividing by the corresponding weight reported on the landing receipt. Coverage rates in the 1981-82 season were very low, 6% for swordfish, 1% for thresher sharks, and 1% for shortfin makos. This was probably due to the newness of the logbook program that contributed to a low logbook return rate and possibly some deliberate misreporting of landings. Coverage rates for other



BOAT NUMBER ______ SKIPPER'S NAME ______ PERMIT NO. ______

FISH AND GAME RECEIPT NO.'S ______ ______ ______ ______

______ ______ ______ ______

| DATE MO/DAY | SET NO. | F & G BLOCK NO. | DEPTH OF WATER (FMS) | NET LENGTH (FMS) | MESH SIZE | BUOY LINE* DEPTH | HOURS NET SOAKED | DRIFT | SET | NUMBER CAUGHT (OTHER THAN ROCKFISH, KINGFISH, AND PERCH) (WHICH MAY BE REPORTED IN POUNDS OR NUMBERS) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | SPECIES | NO. | SPECIES | NO. | SPECIES | NO. |
| | | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | |

* FOR SHARK/SWORDFISH DRIFT GILL NET ONLY

CREW MEMBERS (FOR QUALIFICATION)

| NAME | FISHING LICENSE NO. |
|---|---|
| | |
| | |
| | |

NUMBER AND SPECIES OF FISH LOST TO

☐ MARINE MAMMALS ☐ SHARKS ☐ OTHER

FIGURE 10. Current California Department of Fish and Game logbook used to record catches and fishing effort of drift gill net vessels.

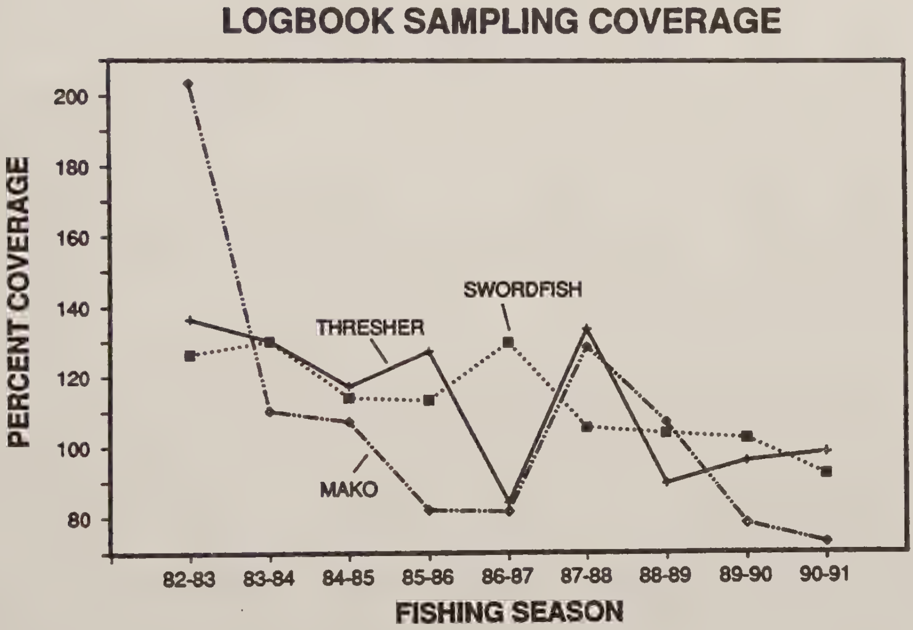


FIGURE 11. Coverage rates for drift gill net logbooks, 1982-83 through 1990-91. Rates are calculated as logged catch/landed weight. Coverage rates for the 1981-82 season were unusually low (6% for swordfish, 1% for common thresher and shortfin mako) and have not been included.

years for each of these species were almost always greater than 100% (Figure 11). Coverage rates over 100% may have been caused by overestimates in the reported logbook catches, or our calculated mean weights may have been biased high and overestimated actual landings. Also, landing receipts with an incorrectly recorded gear code (whether an inadvertent mistake or a conscious effort to subvert catch-ratio regulations) may not have been included in the summaries of drift gill net-caught fish.

### *Swordfish*

Logbook data closely followed landings data showing a peak in the catch during the 1984-85 season of 26,000 swordfish and a decreasing trend to 9000 swordfish in the 1990-91 season (Figure 12a). Catches of swordfish usually began in May to July in each fishing season, peaked in October and November and tapered off in December and January of the following year (Figure 12b).

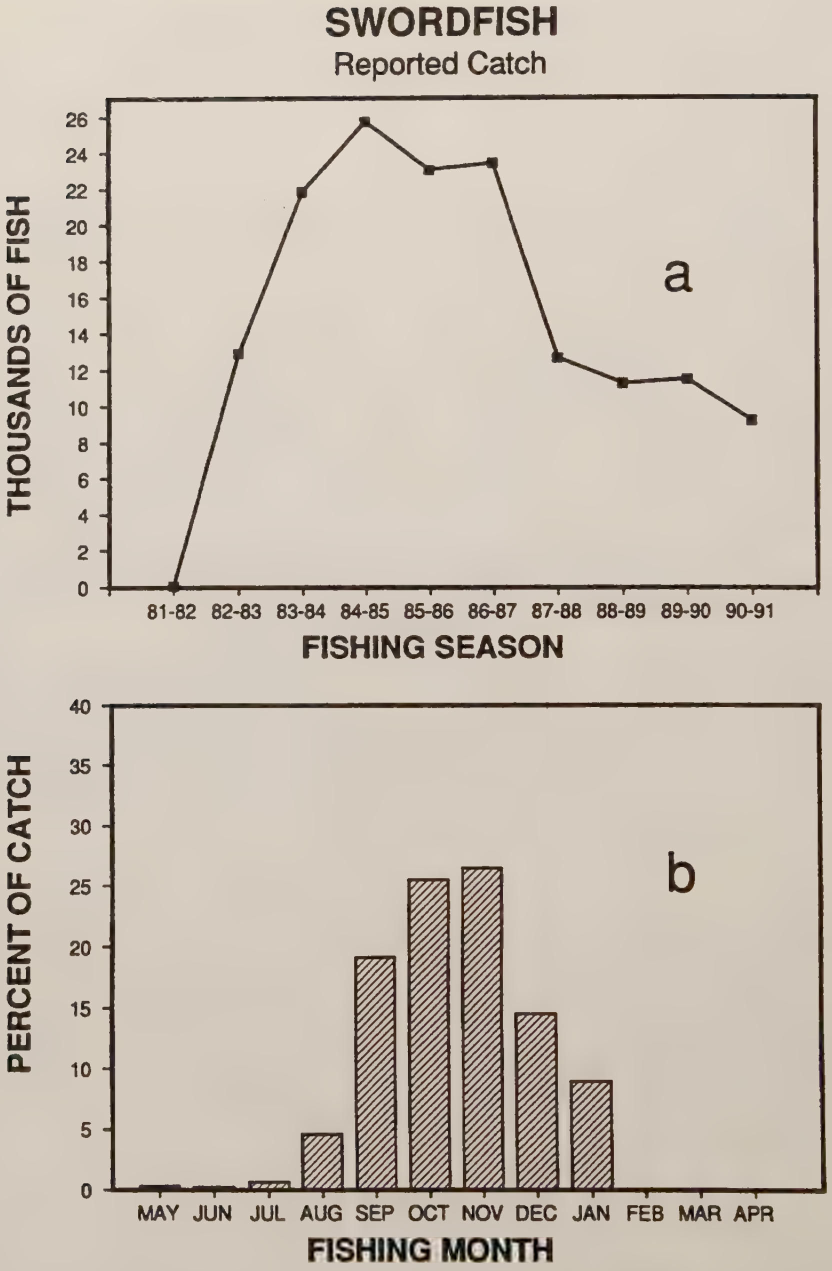


FIGURE 12. Logged catch of swordfish in number of fish by fishing season, 1981-82 through 1990-91 (a) and logged catch by month, all fishing seasons combined (b).

Swordfish were caught mainly in waters between San Diego and San Francisco and within 300 miles of shore (Figure 13). During the 1981-82 and 1982-83 seasons, areas of highest catches were off San Diego and expanded to include some areas around the Channel Islands during the following seasons. Small numbers of swordfish were also caught in areas between San Francisco and the California-Oregon border and within 120 miles of the shoreline. Some catches occurred farther north off Oregon and Washington, but because in some seasons the exact positions were not reported (designated only as off Oregon), they are depicted here in a 1° square at lat. 40° to 41° N (Figure 13).

## *Common Thresher*

The catch of common thresher reported on logbooks in 1981-82 was only 1000 fish, while landings exceeded 2 million lb. In 1982-83, logbook-reported catches climbed to over 20,000 fish and remained relatively high through the 1985-86 season (Figure 14a). Beginning with the 1986-87 season, the Legislature reduced the drift gill net thresher shark fishery to 30 days in May. As a result, mean catches of common thresher dropped to 6000 fish per season. In 1990-91, the Legislature closed the spring drift gill net fishery within 75 miles of shore, thus eliminating the directed thresher shark fishery in California.

When not restricted by closures, the highest proportion of catch was reported during May and June with 50% of the annual catch taken during these 2 months. The remainder of the catch was taken as incidental catch as the drift gill net fishery targeted swordfish during the summer and fall months. During the 10-year period, total catch varied somewhat between seasons, although the rate fluctuated little after the initial months of May and June (Figure 14b).

During the first years, most of the catch of common threshers was concentrated within the Southern California Bight. As the fishery expanded northward in 1982, catches off San Francisco (and north to about the Mendocino Ridge) became an important component of the total catch (Figure 15). A few drift gill net vessels fished Oregon and Washington waters near the Columbia River in 1986 and 1987 and landed 58,000 lb of common thresher in California. An additional 890,000 lb, landed in Oregon and Washington during these 2 years (Stick and Hreha 1988), are not included in our analyses.

## *Pelagic and Bigeye Threshers*

During the 10 fishing seasons 1981-82 to 1990-91, only 624 pelagic and 1891 bigeye threshers were reported on logbooks, although more may have been misreported as common threshers. A high proportion of the pelagic thresher catch was reported for May (Figure 16). They were also frequently caught in October

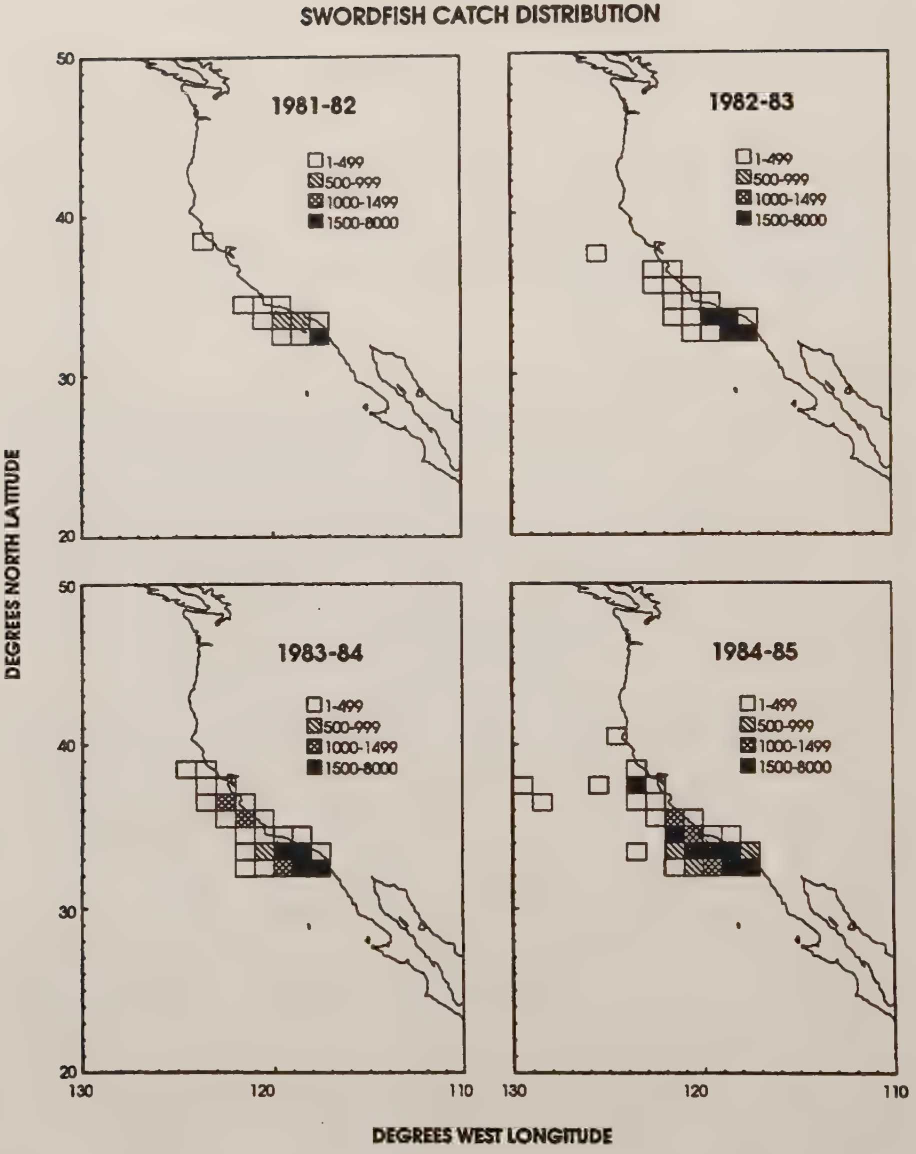

SWORDFISH CATCH DISTRIBUTION
1981-82
1982-83
1983-84
1984-85
□ 1-499
▨ 500-999
▦ 1000-1499
■ 1500-8000
DEGREES NORTH LATITUDE
50
40
30
20
130
120
110
DEGREES WEST LONGITUDE

FIGURE 13a. Distribution of swordfish catches by 1° quadrangle from California drift gill net logbook data for the 1981-82 through 1984-85 fishing seasons.

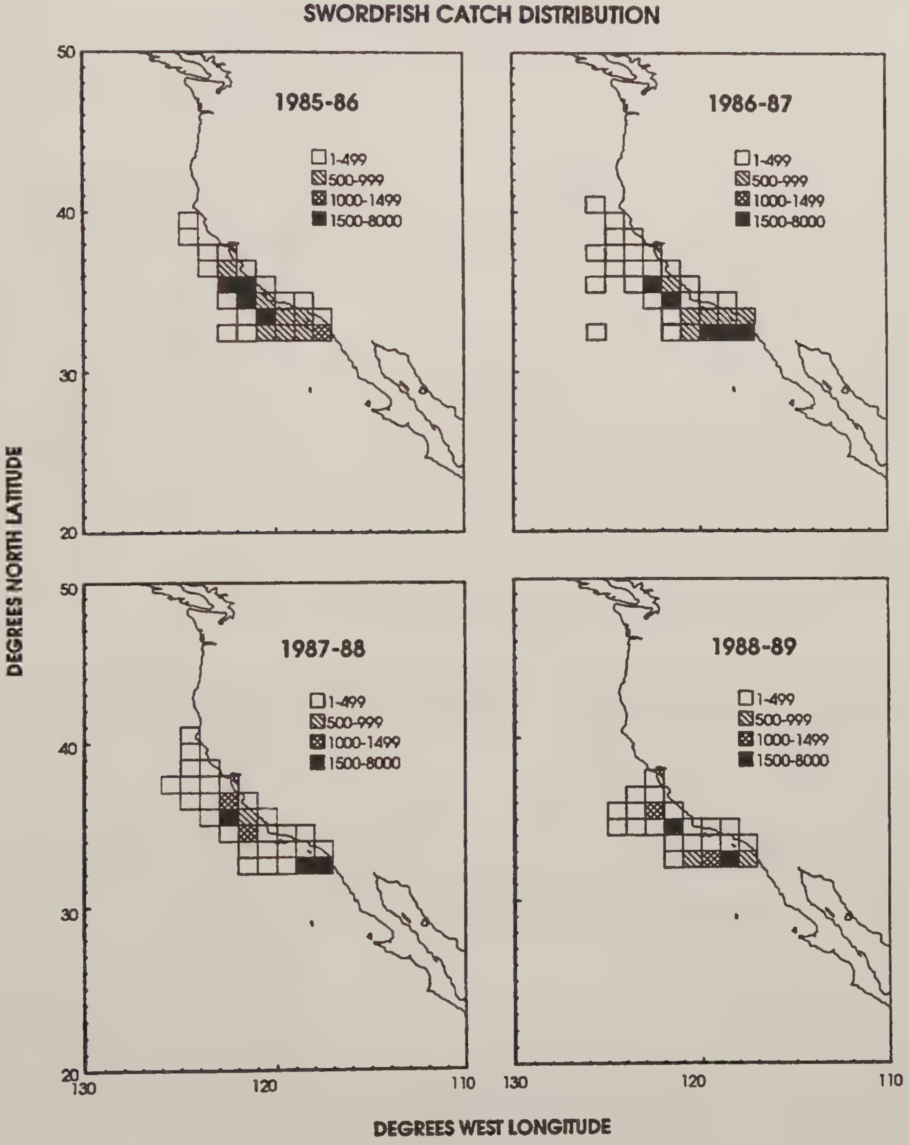

SWORDFISH CATCH DISTRIBUTION
1985-86
1986-87
1987-88
1988-89
1-499
500-999
1000-1499
1500-8000
50
40
30
20
130
120
110
DEGREES NORTH LATITUDE
DEGREES WEST LONGITUDE

FIGURE 13b. Distribution of swordfish catches by 1° quadrangle from California drift gill net logbook data for the 1985-86 through 1988-89 fishing seasons.

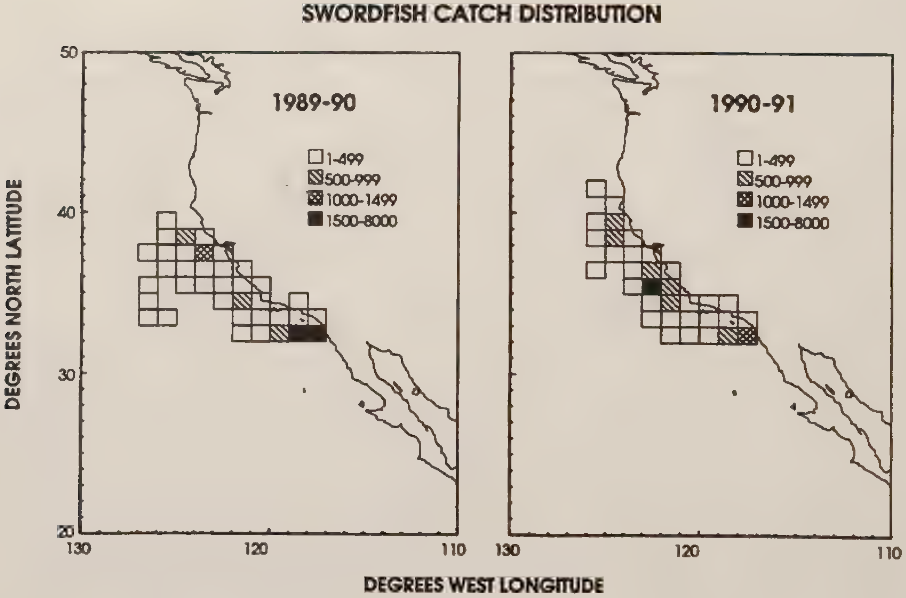

SWORDFISH CATCH DISTRIBUTION
1989-90
1990-91
□ 1-499
▨ 500-999
▩ 1000-1499
■ 1500-8000
DEGREES NORTH LATITUDE
50
40
30
20
130
120
110
DEGREES WEST LONGITUDE

FIGURE 13c. Distribution of swordfish catches by 1° quadrangle from California drift gill net logbook data for the 1989-90 and 1990-91 fishing seasons.

through January. Bigeye threshers were caught in August to November with a peak in September (Figure 17). Catches of both species were concentrated in the southern areas of the Southern California Bight (Figures 18 and 19).

## *Shortfin Mako*

Reported catches of shortfin mako peaked in the 1982-83 season at 19,500 fish and again in the 1986-87 season at 13,500 fish (Figure 20a). The 1981-82 reported catch (299 shortfin makos) was apparently low, because landings of 250,000 lb were reported on landing receipts. Average catch in the remaining years was just over 9300 fish or about 318,000 lb. Between the 1981-82 and 1988-89 seasons, shortfin makos were caught incidentally to thresher shark and swordfish from May to January, although the greatest portion was taken during July through September (Figure 20b). The proportion of catch in May declined substantially after the 1989 drift gill net fishing closure within 75 miles of shore during the spring. Overall, catches for the 10 years of data peaked in August and declined through winter months (Figure 20b).

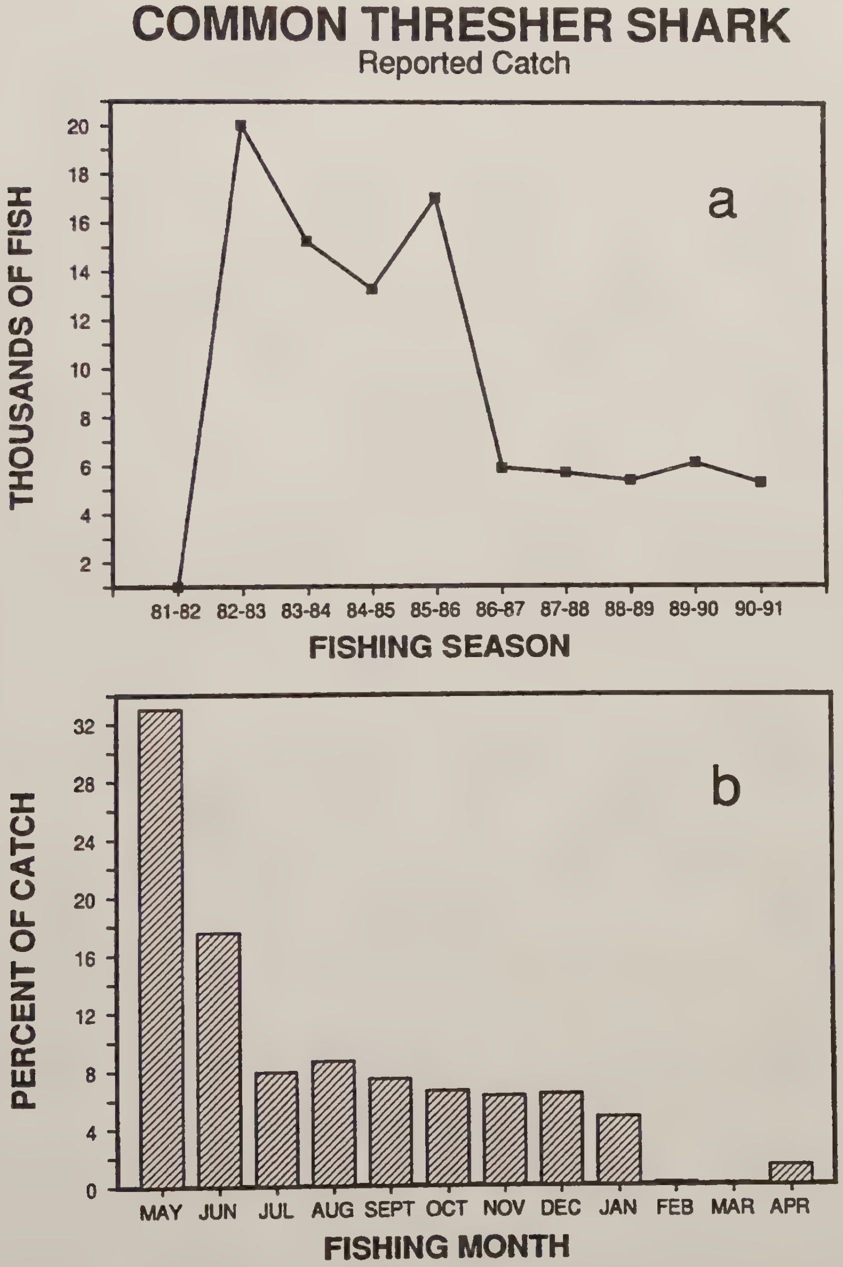


FIGURE 14. Logged catch of common thresher in number of fish by fishing season, 1981-82 through 1990-91 (a) and logged catch by month, all fishing seasons combined (b).

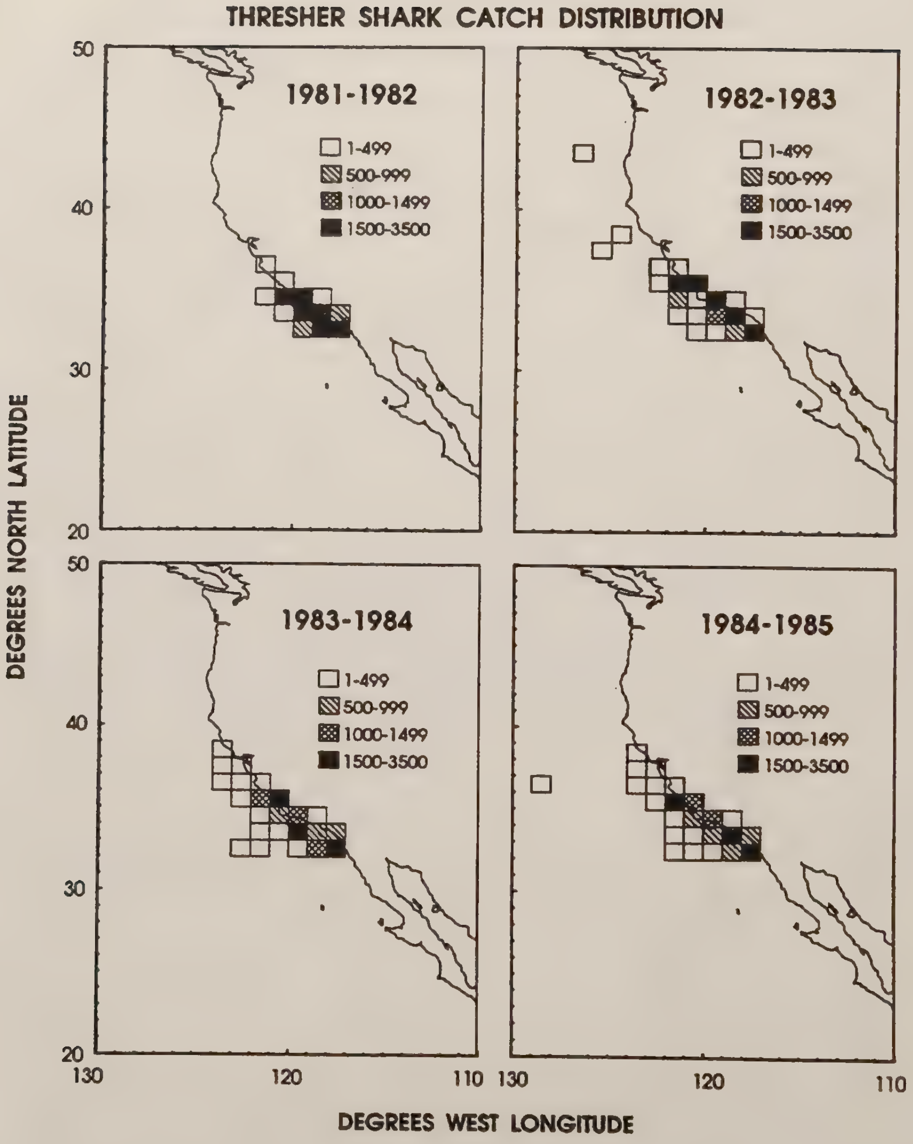

THRESHER SHARK CATCH DISTRIBUTION
1981-1982
1982-1983
1983-1984
1984-1985
1-499
500-999
1000-1499
1500-3500
50
40
30
20
130
120
110
DEGREES NORTH LATITUDE
DEGREES WEST LONGITUDE

FIGURE 15a. Distribution of common thresher catches by 1° quadrangle from California drift gill net logbook data for the 1981-82 through 1984-85 fishing seasons.

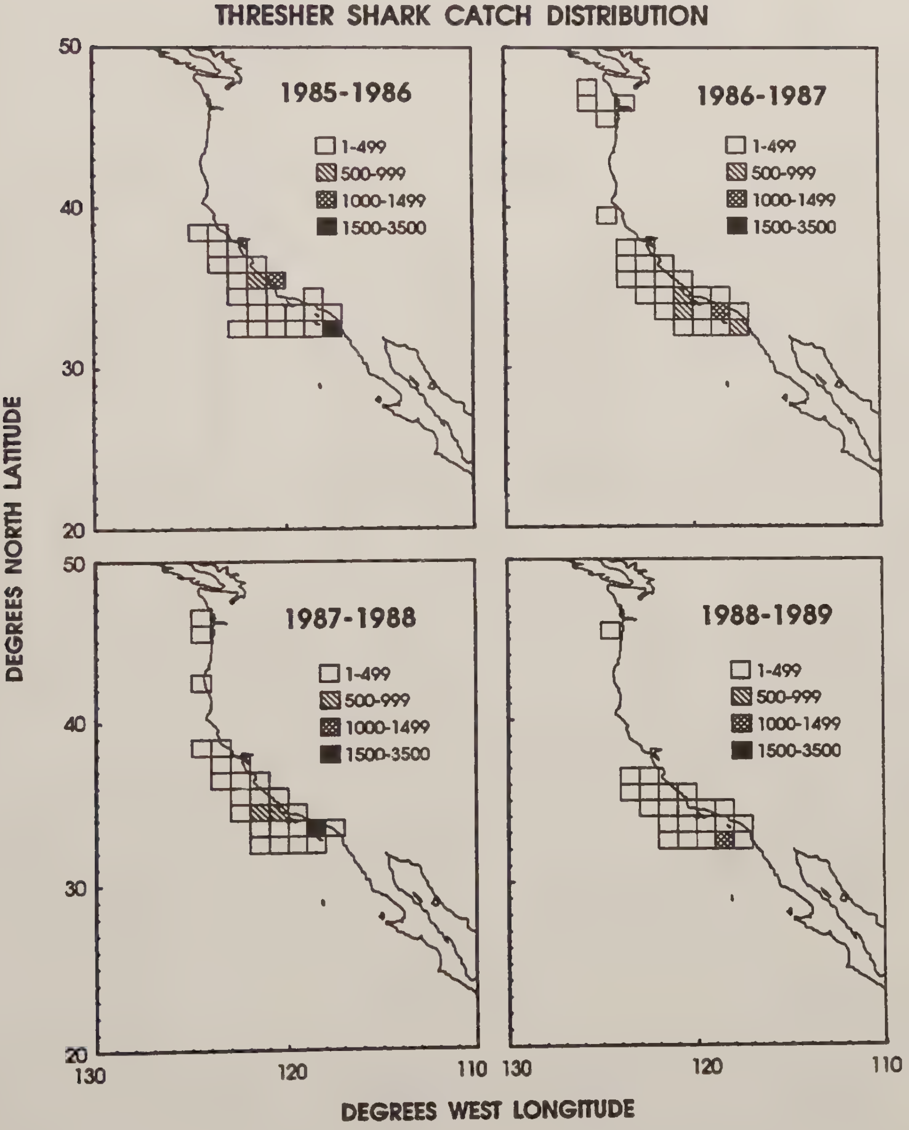

THRESHER SHARK CATCH DISTRIBUTION
1985-1986
1986-1987
1987-1988
1988-1989
□ 1-499
▨ 500-999
▩ 1000-1499
■ 1500-3500
DEGREES NORTH LATITUDE
50
40
30
20
DEGREES WEST LONGITUDE
130
120
110

FIGURE 15b. Distribution of common thresher catches by 1° quadrangle from California drift gill net logbook data for the 1985-86 through 1988-89 fishing seasons.

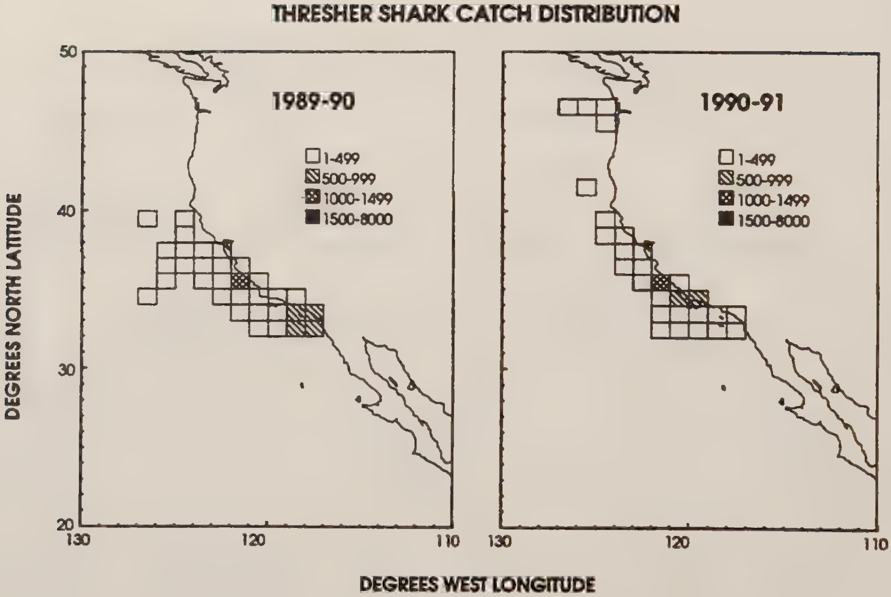

THRESHER SHARK CATCH DISTRIBUTION
1989-90
1990-91
1-499
500-999
1000-1499
1500-8000
DEGREES NORTH LATITUDE
50
40
30
20
130
120
110
DEGREES WEST LONGITUDE

FIGURE 15c. Distribution of common thresher catches by 1° quadrangle from California drift gill net logbook data for the 1989-90 and 1990-91 fishing seasons.

Greatest shortfin mako catches were reported within the Southern California Bight. Sparse catches were recorded northward to about San Francisco in the early years following the 1982-83 season. Shortfin mako catches were rarely reported north of Cape Mendocino or beyond 200 miles from shore (Figure 21).

## *Opah*

Logbook catch data for opah closely followed landings data and showed peaks of 4300 fish in the 1984-85 season and 4100 fish in the 1985-86 season. After 1986, opah catches declined to a low of 600 fish in the 1988-89 season, then increased to 1300 fish in the 1989-90 season and 1100 fish in the 1990-91 season. Monthly catch summaries peaked in May (Figure 22), especially during the 1986-87 and 1988-89 seasons when 46% to 49% of the catch was reported in May. For the balance of the year, catches were rather evenly distributed during June to January with a peak in August. Opah catches occur throughout the range of the fishery, but are highest in the south (Figure 23).

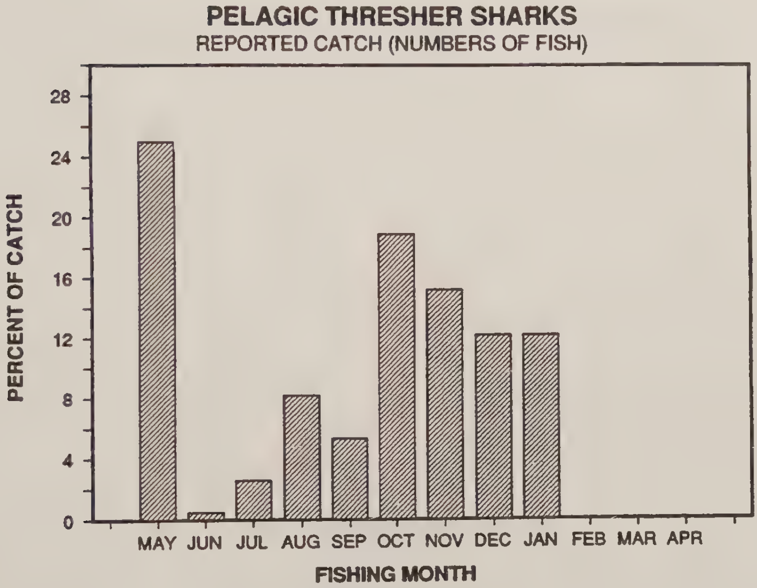


FIGURE 16. Logged catch of pelagic thresher in number of fish by month, all fishing seasons, 1981-82 through 1990-91 combined.

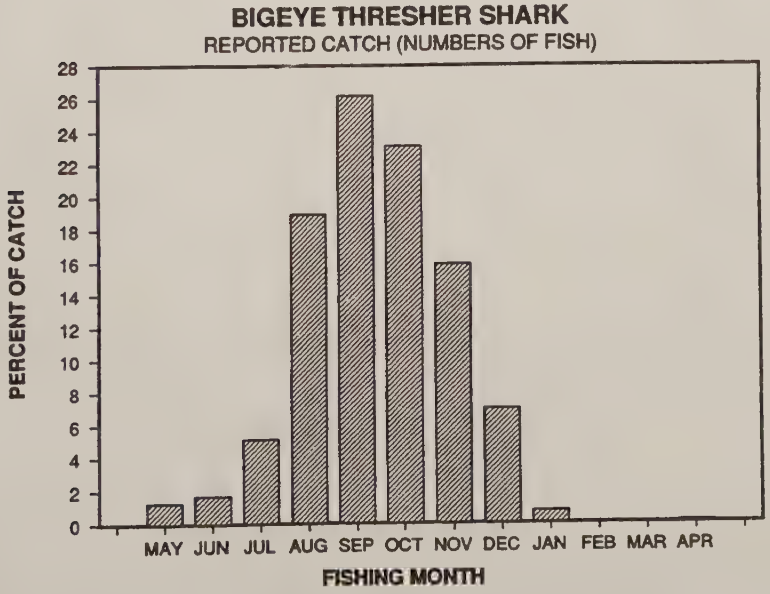


FIGURE 17. Logged catch of bigeye thresher in number of fish by month, all fishing seasons, 1981-82 through 1990-91 combined.

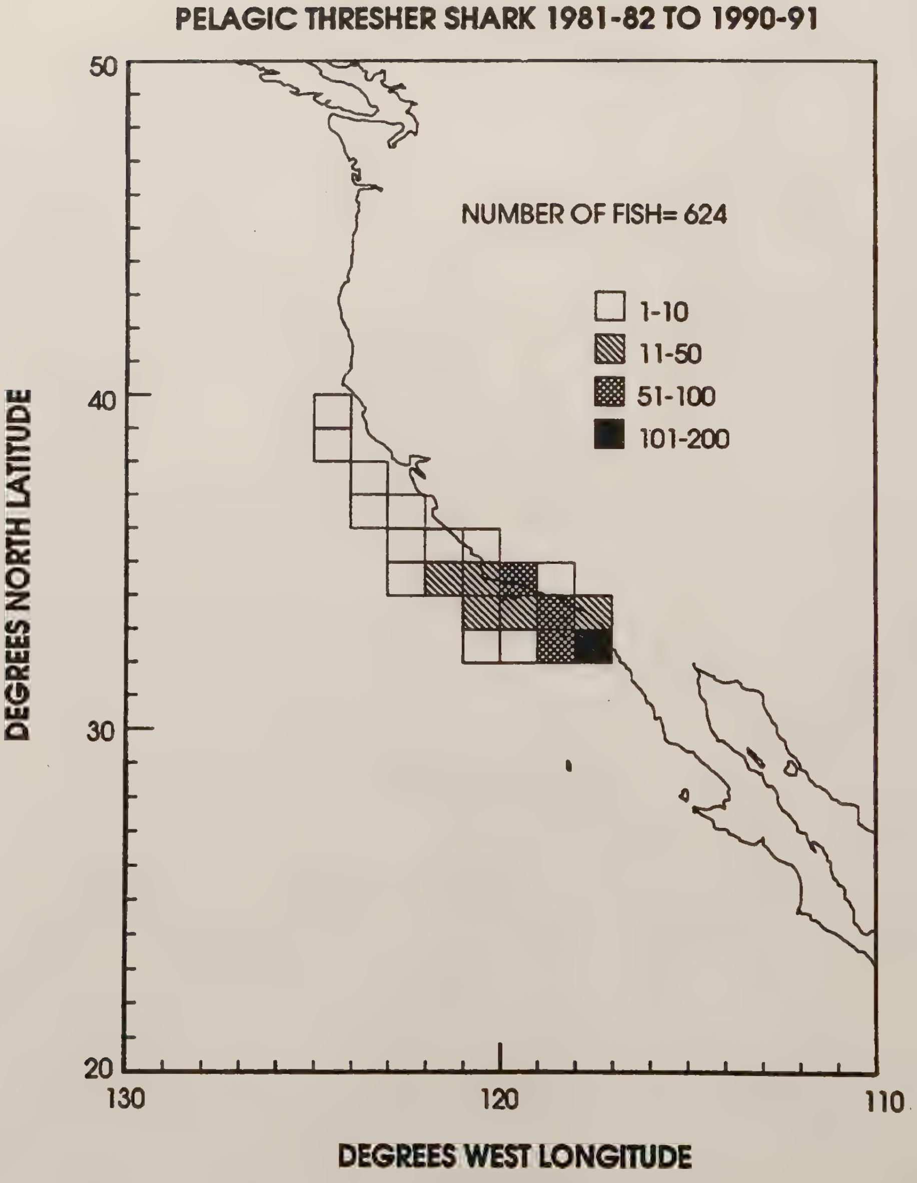

PELAGIC THRESHER SHARK 1981-82 TO 1990-91
NUMBER OF FISH= 624
1-10
11-50
51-100
101-200
50
40
30
20
130
120
110
DEGREES NORTH LATITUDE
DEGREES WEST LONGITUDE

FIGURE 18. Distribution of pelagic thresher catches by 1° quadrangle from California drift gill net logbook data for the 1981-82 through 1990-91 fishing seasons.

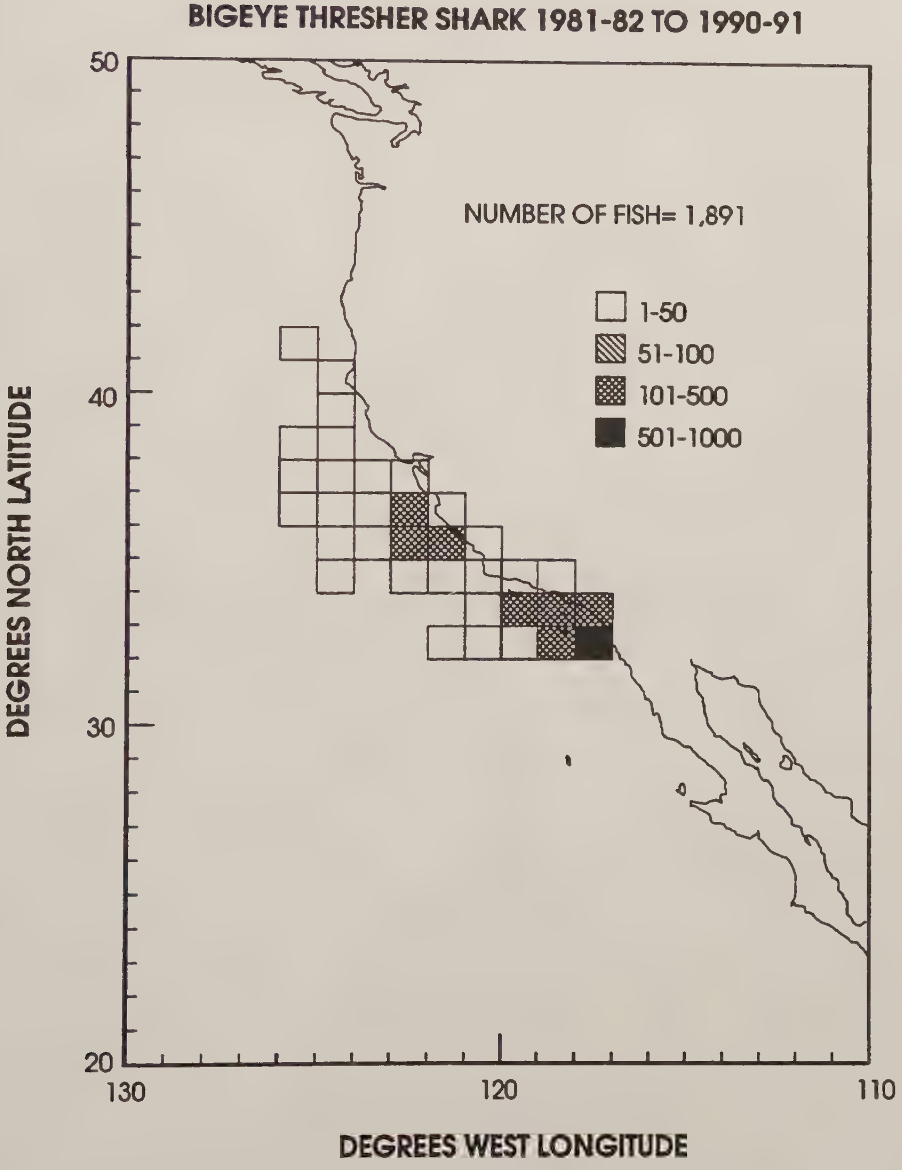

BIGEYE THRESHER SHARK 1981-82 TO 1990-91
NUMBER OF FISH= 1,891
☐ 1-50
▨ 51-100
▩ 101-500
■ 501-1000
50
40
30
20
130
120
110
DEGREES NORTH LATITUDE
DEGREES WEST LONGITUDE

FIGURE 19. Distribution of bigeye thresher catches by 1° quadrangle from California drift gill net logbook data for the 1981-82 through 1990-91 fishing seasons.

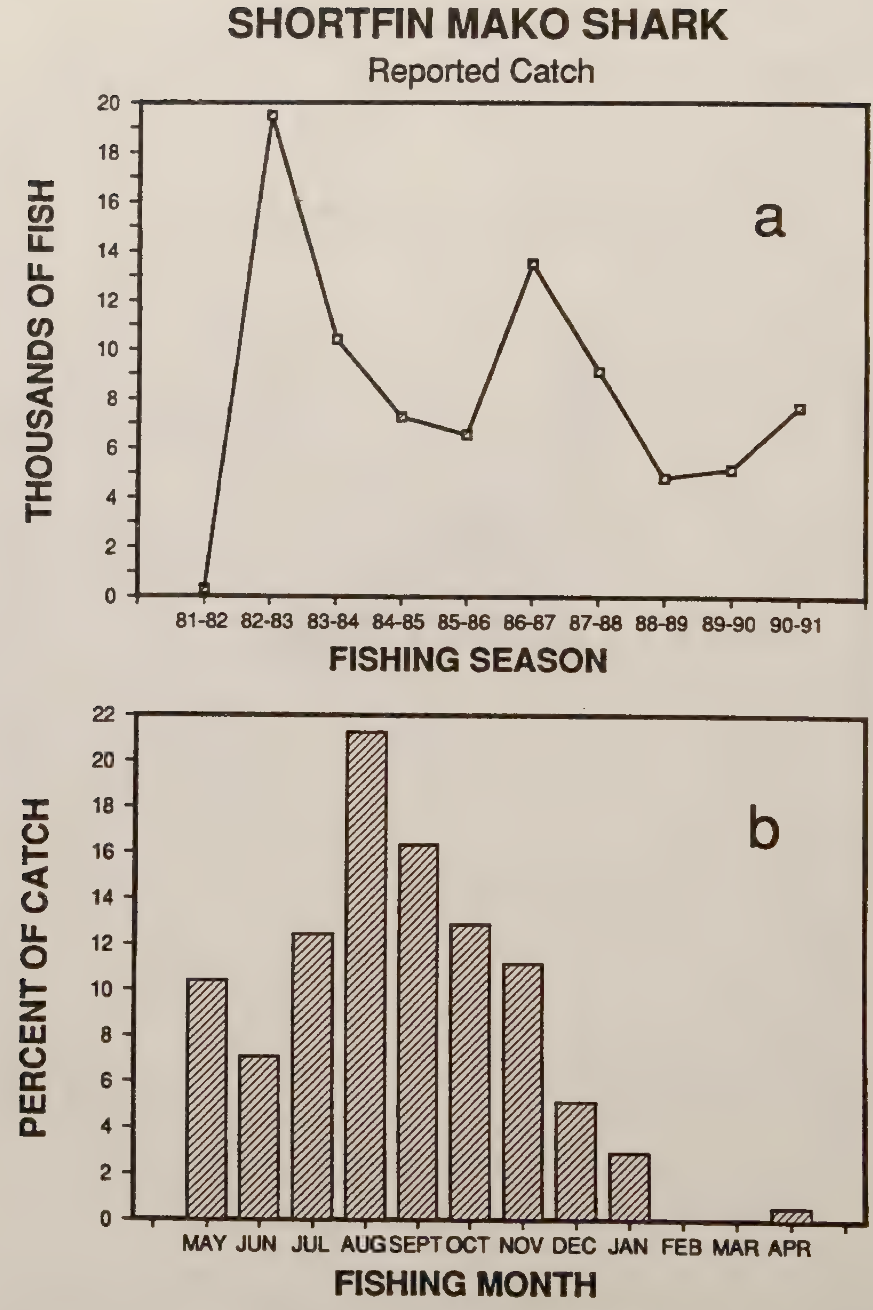


FIGURE 20. Logged catch of shortfin mako in number of fish by fishing season, 1981-82 through 1990-91 (a) and logged catch by month, all fishing seasons combined (b).

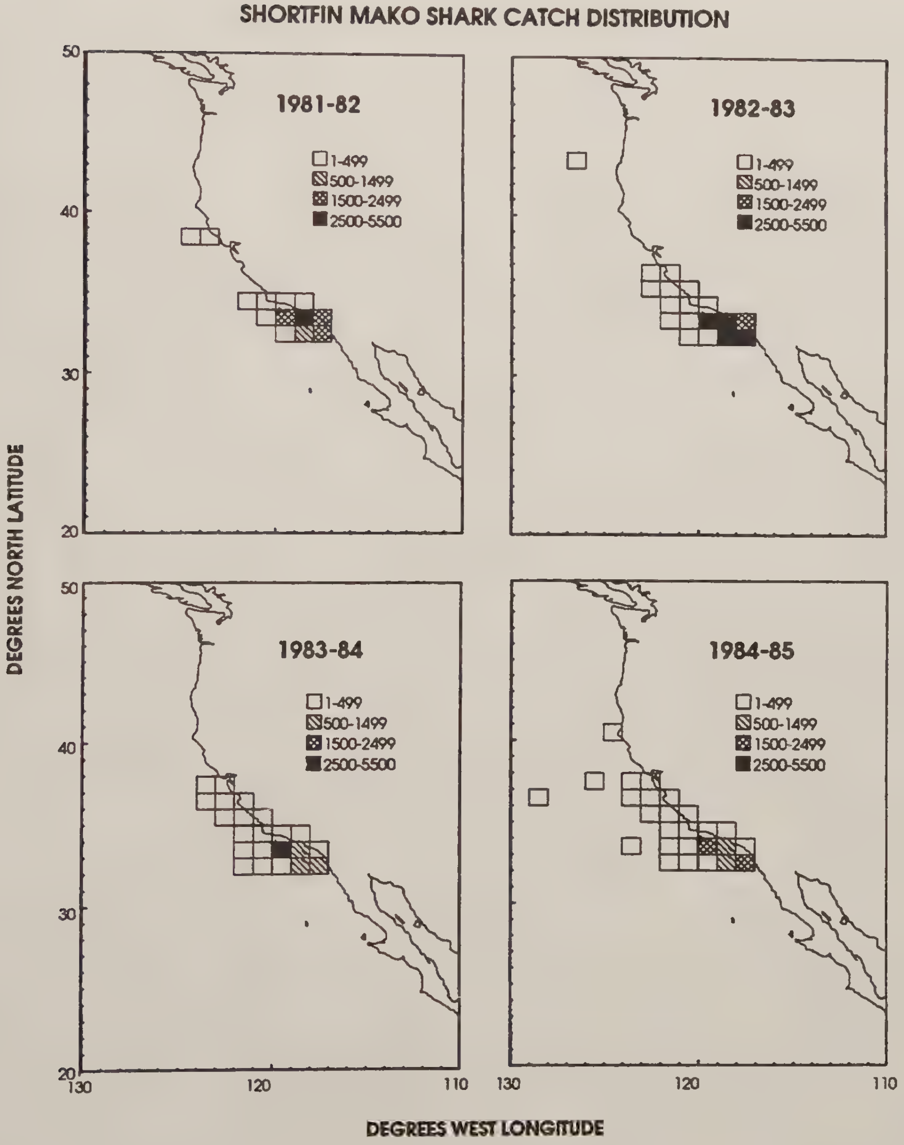

SHORTFIN MAKO SHARK CATCH DISTRIBUTION
1981-82
1982-83
1983-84
1984-85
1-499
500-1499
1500-2499
2500-5500
DEGREES NORTH LATITUDE
50
40
30
20
130
120
110
DEGREES WEST LONGITUDE

FIGURE 21a. Distibution of shortfin mako catches by 1° quadrangle from California drift gill net logbook data for the 1981-82 through 1984-84 fishing seasons.

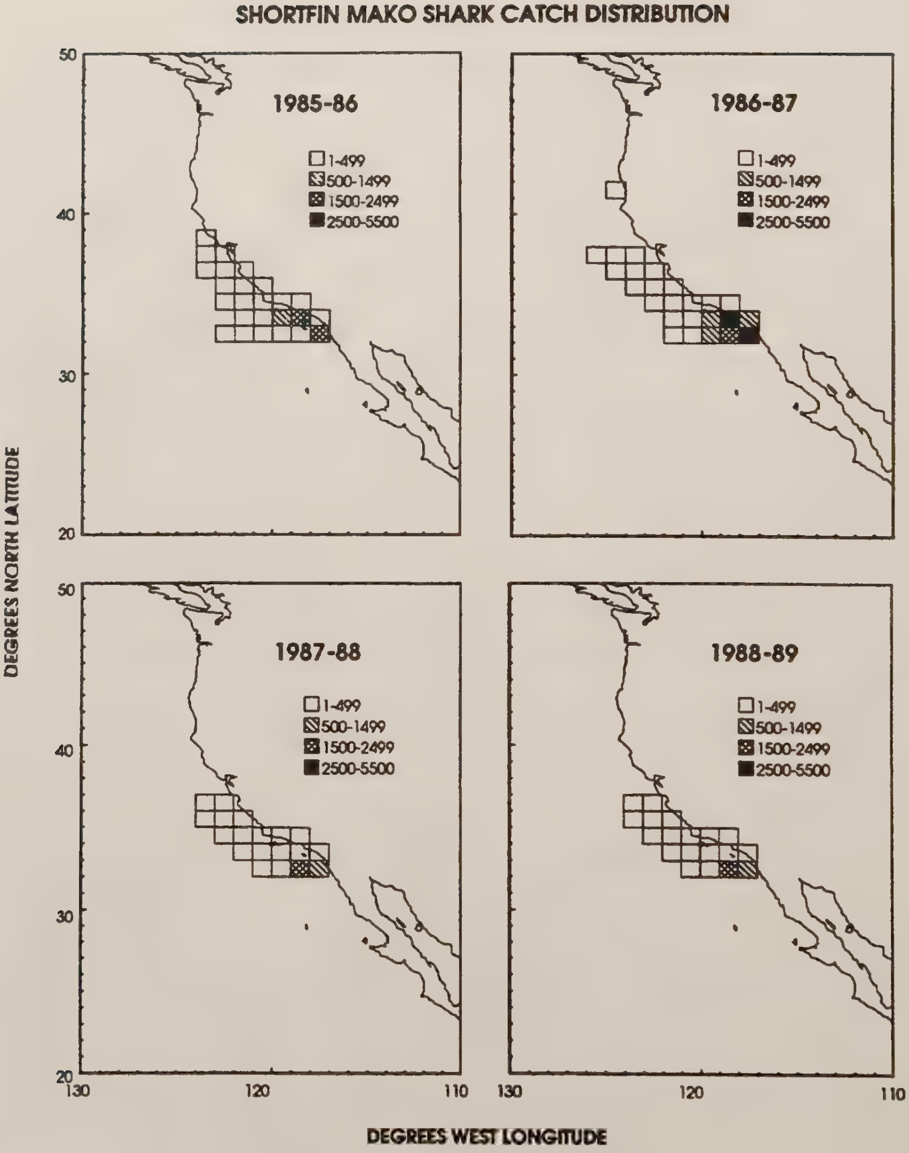

SHORTFIN MAKO SHARK CATCH DISTRIBUTION
1985-86
1986-87
1987-88
1988-89
☐ 1-499
▨ 500-1499
▩ 1500-2499
■ 2500-5500
50
40
30
20
130
120
110
DEGREES NORTH LATITUDE
DEGREES WEST LONGITUDE

FIGURE 21b. Distribution of shortfin mako catches by 1° quadrangle from California drift gill net logbook data for the 1985-86 through 1988-89 fishing seasons.

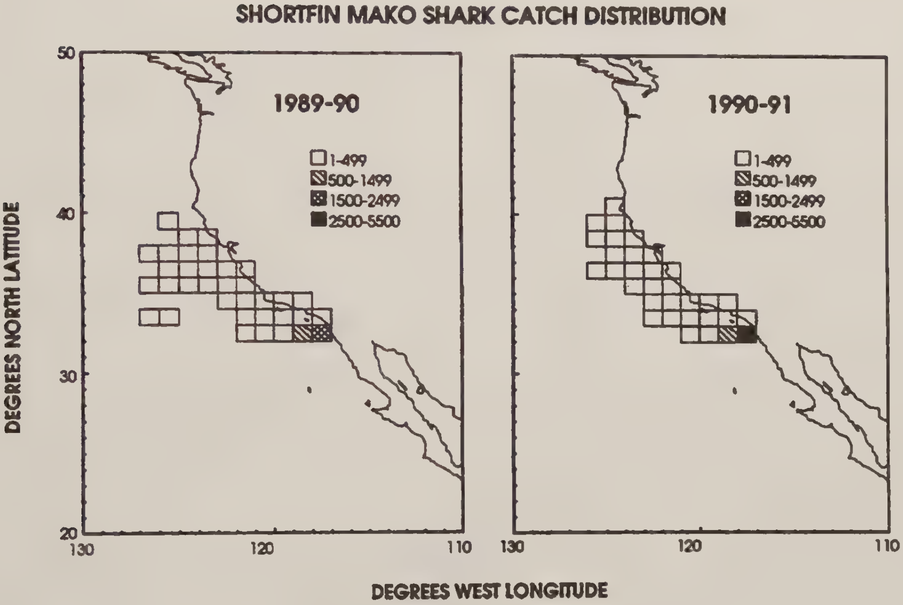

SHORTFIN MAKO SHARK CATCH DISTRIBUTION
1989-90
1990-91
☐1-499
▨500-1499
▩1500-2499
■2500-5500
DEGREES NORTH LATITUDE
50
40
30
20
130
120
110
DEGREES WEST LONGITUDE

FIGURE 21c. Distribution of shortfin mako catches by 1°quadrangle from California drift gill net logbook data for the 1989-90 and 1990-91 fishing seasons.

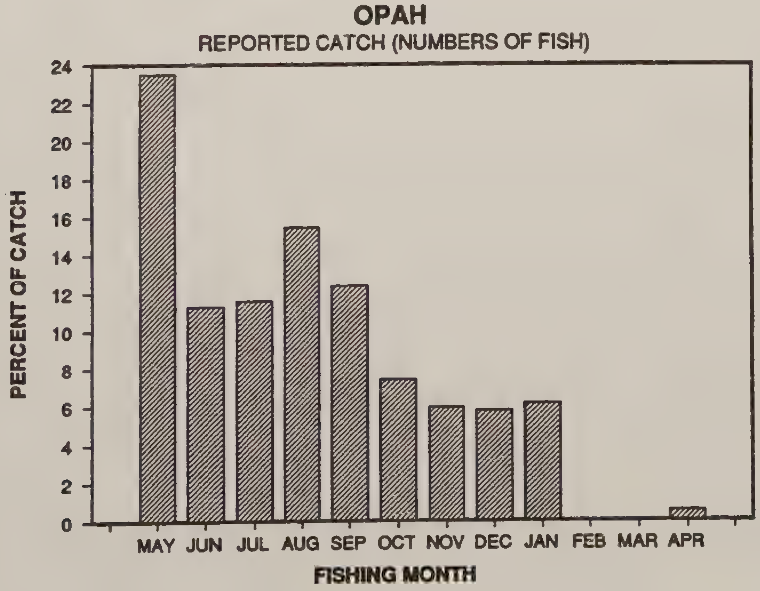


FIGURE 22. Logged catch of opah in number of fish by month, all fishing seasons, 1981-82 through 1990-91 combined.

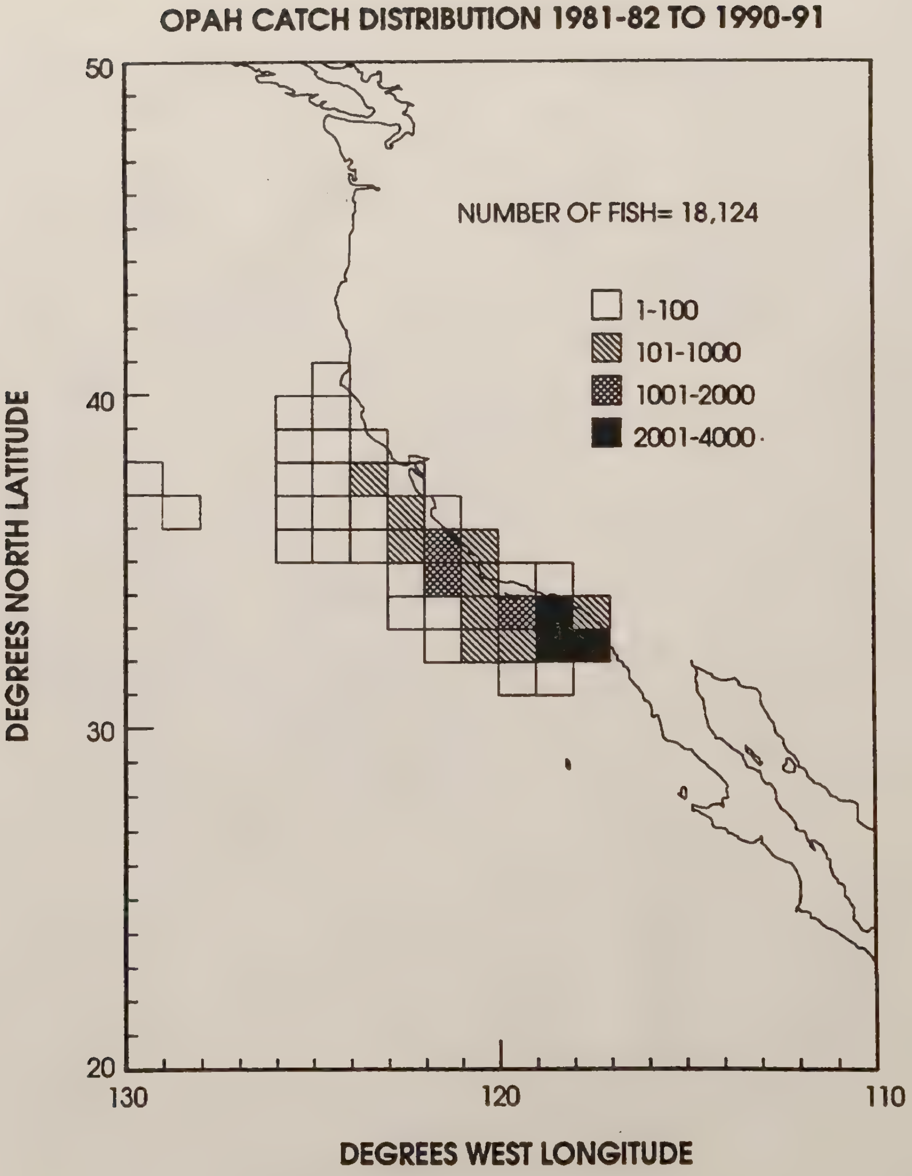

OPAH CATCH DISTRIBUTION 1981-82 TO 1990-91
NUMBER OF FISH= 18,124
□ 1-100
▨ 101-1000
▩ 1001-2000
■ 2001-4000
50
40
30
20
130
120
110
DEGREES NORTH LATITUDE
DEGREES WEST LONGITUDE

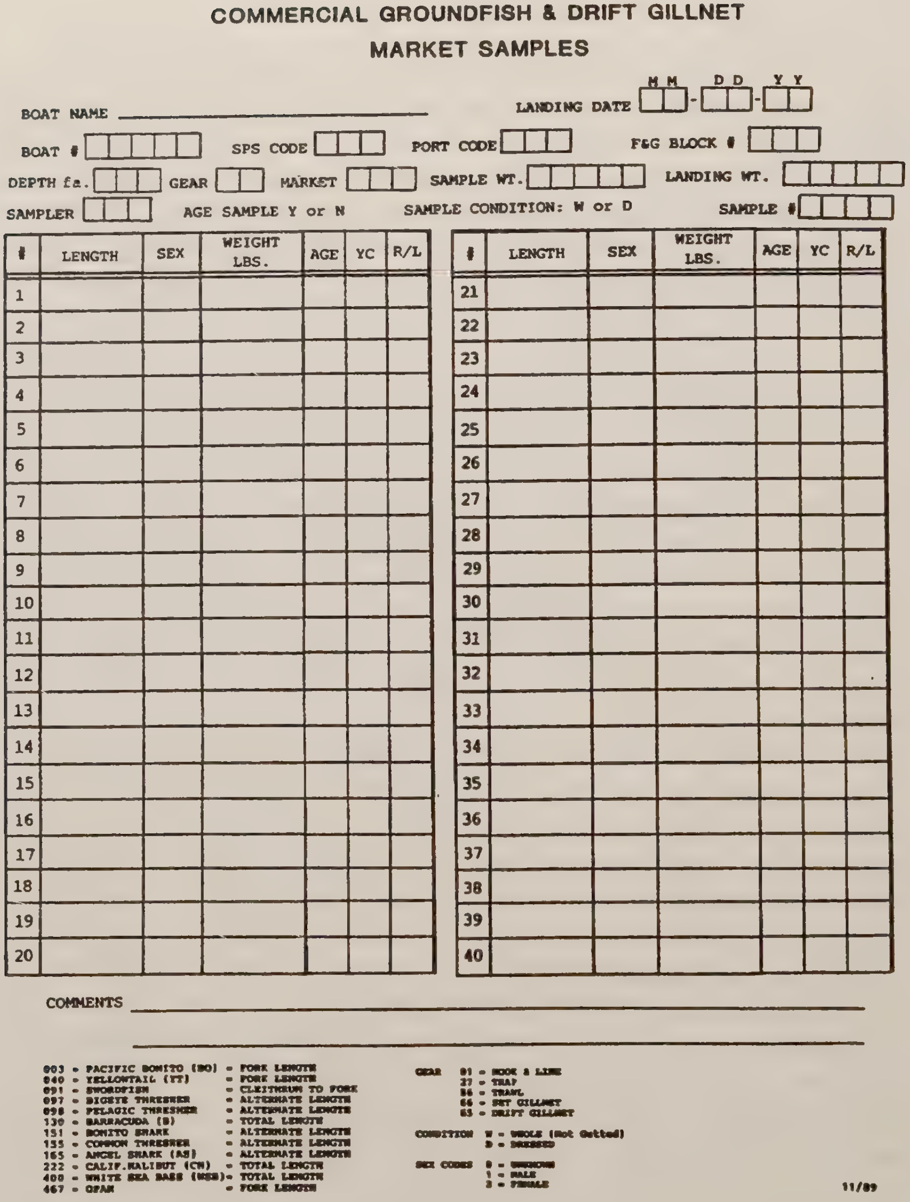
FIGURE 23. Distribution of opah catches by 1° quadrangle from California drift gill net logbook data for the 1981-82 through 1990-91 fishing seasons.

## SIZE COMPOSITION

The CDFG began a program in 1981 to sample the landings of drift gill net vessels as catches were unloaded at commercial markets (Odemar 1982). Samples were taken at ports as far north as San Francisco and as far south as San Diego. While the majority of the samples were from catches made in the Southern California Bight, some samples were from catches made as far north as Oregon and Washington, as far south as the California-Mexico border, or as far as 250 miles offshore. Port samplers recorded lengths and weights of swordfish, thresher sharks, and shortfin makos (Figure 24). Sharks and swordfish were dressed at sea (headed and eviscerated), therefore lengths of these species measured at the wholesalers were alternate lengths (AL). Alternate length for swordfish was measured from the anterior margin of the cleithrum to the fork of the tail; for sharks, AL was measured from the origin of the first dorsal fin to the origin of the second dorsal fin (Figure 25). Measurements were taken with calipers to the nearest millimeter.

Lengths and weights, as well as other biological parameters (sex, pup counts, etc.), were recorded occasionally for other species (tunas, opah, louvar, etc.). Although size-composition samples were taken of many species of fish from landings at commercial fish markets, the vast majority of the samples were of swordfish, thresher sharks (common, pelagic, and bigeye) and shortfin mako (Table 4).

Size-composition coverage rates were estimated as the number of fish measured divided by the number of fish reported in logbooks. Coverage rates were highest for swordfish in all seasons except 1982-83 and 1989-90 when thresher sharks or shortfin mako were targeted by samplers (Figure 26). Swordfish samples rose from a low of 207 in the 1981-82 season to a high of 4972 in the 1986-87 season and dropped to 1029 in the 1990-91 season. The highest swordfish size-composition coverage rates (28%) were obtained during the 1988-89 season. Common thresher samples decreased from a high of 1568 in the 1983-84 season to a low of 665 in the 1987-88 season. Common thresher size-composition coverage rates were highest during the 1989-90 season. Shortfin mako samples rose from a low of three in the 1981-82 season to a high of 1097 in the 1989-90 season; size-composition coverage rates were highest during the 1989-90 season. Size-composition coverage rates estimated for the 1981-82 season were unrealistically high for swordfish (356%) and thresher sharks (106%) due to low logbook coverage rates. Coverage rates for shortfin mako were 1% for the 1981-82 and 1982-83 seasons.



COMMERCIAL GROUNDFISH & DRIFT GILLNET
MARKET SAMPLES

BOAT NAME ____________________
LANDING DATE ☐☐-☐☐-☐☐ (M M - D D - Y Y)

BOAT # ☐☐☐☐☐ SPS CODE ☐☐☐ PORT CODE ☐☐☐ F&G BLOCK # ☐☐☐

DEPTH fa. ☐☐☐ GEAR ☐☐ MARKET ☐☐☐ SAMPLE WT. ☐☐☐☐☐ LANDING WT. ☐☐☐☐☐

SAMPLER ☐☐☐ AGE SAMPLE Y or N SAMPLE CONDITION: W or D SAMPLE # ☐☐☐☐

| # | LENGTH | SEX | WEIGHT LBS. | AGE | YC | R/L | # | LENGTH | SEX | WEIGHT LBS. | AGE | YC | R/L |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | | | | | | | 21 | | | | | | |
| 2 | | | | | | | 22 | | | | | | |
| 3 | | | | | | | 23 | | | | | | |
| 4 | | | | | | | 24 | | | | | | |
| 5 | | | | | | | 25 | | | | | | |
| 6 | | | | | | | 26 | | | | | | |
| 7 | | | | | | | 27 | | | | | | |
| 8 | | | | | | | 28 | | | | | | |
| 9 | | | | | | | 29 | | | | | | |
| 10 | | | | | | | 30 | | | | | | |
| 11 | | | | | | | 31 | | | | | | |
| 12 | | | | | | | 32 | | | | | | |
| 13 | | | | | | | 33 | | | | | | |
| 14 | | | | | | | 34 | | | | | | |
| 15 | | | | | | | 35 | | | | | | |
| 16 | | | | | | | 36 | | | | | | |
| 17 | | | | | | | 37 | | | | | | |
| 18 | | | | | | | 38 | | | | | | |
| 19 | | | | | | | 39 | | | | | | |
| 20 | | | | | | | 40 | | | | | | |

COMMENTS ____________________

| | | |
|---|---|---|
| 003 - PACIFIC BONITO (BO) | - FORK LENGTH | |
| 040 - YELLOWTAIL (YT) | - FORK LENGTH | |
| 091 - SWORDFISH | - CLEITHRUM TO FORK | |
| 097 - BIGEYE THRESHER | - ALTERNATE LENGTH | |
| 098 - PELAGIC THRESHER | - ALTERNATE LENGTH | |
| 130 - BARRACUDA (B) | - TOTAL LENGTH | |
| 151 - BONITO SHARK | - ALTERNATE LENGTH | |
| 155 - COMMON THRESHER | - ALTERNATE LENGTH | |
| 165 - ANGEL SHARK (AS) | - ALTERNATE LENGTH | |
| 222 - CALIF.HALIBUT (CH) | - TOTAL LENGTH | |
| 400 - WHITE SEA BASS (WSB) | - TOTAL LENGTH | |
| 467 - OPAH | - FORK LENGTH | |

GEAR
01 - HOOK & LINE
27 - TRAP
56 - TRAWL
66 - SET GILLNET
65 - DRIFT GILLNET

CONDITION
W - WHOLE (Not Gutted)
D - DRESSED

SEX CODES
0 - UNKNOWN
1 - MALE
2 - FEMALE

11/89

FIGURE 24. Current California Department of Fish and Game sampling form used to record fish measurements from California drift gill net landings.

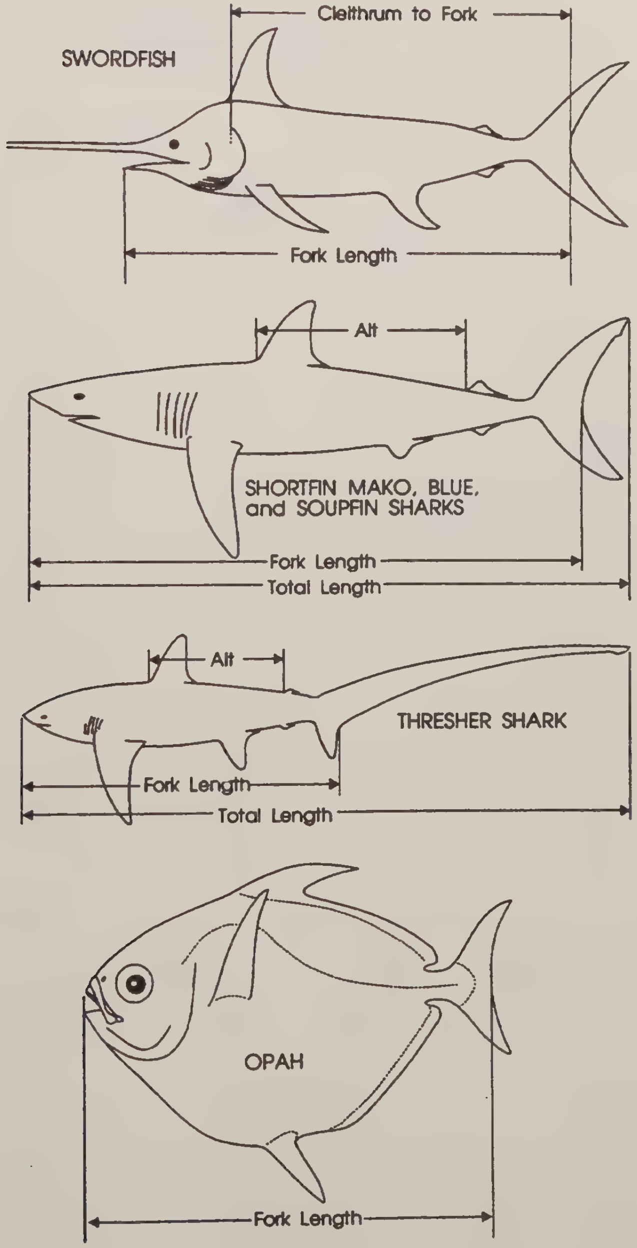

SWORDFISH
Cleithrum to Fork
Fork Length
Alt
SHORTFIN MAKO, BLUE, and SOUPFIN SHARKS
Fork Length
Total Length
Alt
THRESHER SHARK
Fork Length
Total Length
OPAH
Fork Length

FIGURE 25. Alternate length measurements of swordfish, thresher sharks, other sharks, and opah recorded by samplers of California drift gill net landings.

TABLE 4. Numbers and lengths of fishes by species taken in the California drift gill net fishery and sampled at California fish markets during the 1981-82 through 1990-91 fishing seasons. AL=alternate length, FL=fork length.

| Species | Number measured | Length (cm) | |
|---|---|---|---|
| | | Mean | Range |
| Sharks | | | |
| Angel shark, Pacific | 48 | 11.6 (AL) | 9-13 (AL) |
| Blacktip shark | 1 | 118.0 (AL) | 118 (AL) |
| Blue shark | 7 | 77.3 (AL) | 68-105 (AL) |
| Hammerhead shark | 16 | 91.2 (AL) | 78-102 (AL) |
| Mako, shortfin | 5,659 | 46.8 (AL) | 6-134 (AL) |
| Salmon shark | 9 | 93.2 (AL) | 83-98 (AL) |
| Soupfin shark | 32 | 56.8 (AL) | 38-81 (AL) |
| Thresher, bigeye | 468 | 53.0 (AL) | 22-104 (AL) |
| Thresher, common | 9,646 | 60.4 (AL) | 12-136 (AL) |
| Thresher, pelagic | 116 | 64.1 (AL) | 28-100 (AL) |
| White shark | 2 | 88.5 (AL) | 87-90 (AL) |
| Other fishes | | | |
| Albacore | 214 | 102.9 (FL) | 50-133 (FL) |
| Bonito, Pacific | 2 | 69.5 (FL) | 69-70 (FL) |
| Louvar | 142 | 101.5 (FL) | 48-163 (FL) |
| Opah | 1,967 | 99.3 (FL) | 10-242 (FL) |
| Swordfish | 22,870 | 143.8 (AL) | 37-250 (AL) |
| Tuna, bigeye | 58 | 128.7 (FL) | 92-161 (FL) |
| Tuna, yellowfin | 27 | 138.3 (FL) | 96-191 (FL) |

## Swordfish

The sizes of swordfish sampled during the 1981-82 through 1990-91 fishing seasons (22,870 fish measured) ranged from 37 to 250 cm AL with a mean of 144 cm AL (Table 4; Figure 27). Fish reported as less than 47 cm were considered errors in measurement or measurements of shark-damaged fish and were not included in our summaries. The bulk of the measurements were between 100 and 195 cm. By year, the means varied between 128 and 152 cm, with peaks in

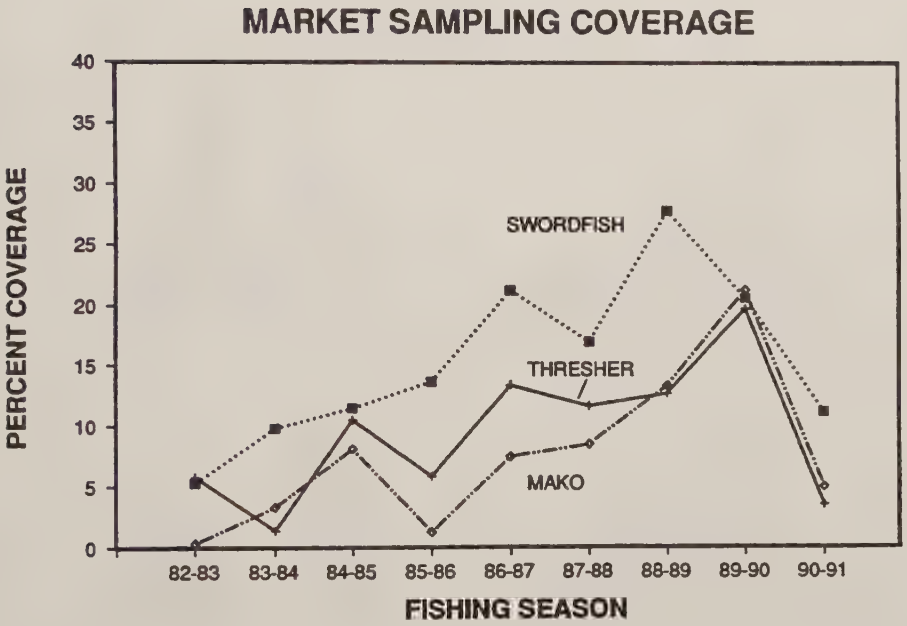


FIGURE 26. Coverage rates for market sampling of swordfish, common thresher, and shortfin mako. Coverage rates for the 1981-82 season were unrealistically high for swordfish (356%) and common thresher (106%) due to low logbook coverage rates, while shortfin mako rates were at 1% and are not presented.

1982-83, 1985-86, and 1988-89 (Figure 28). Larger swordfish (150 to 160 cm AL) tended to be caught off the northern California and Oregon coasts, with smaller fish (130 to 145 cm AL) taken farther south (Figure 29). The primary mode of fish caught north of lat. 35°N tended to be 2 to 5 cm larger than that of fish caught south of that line. Also, the average weights of fish caught north of lat. 35°N were as much as 17 kg (dressed weight) more than fish caught farther south. Swordfish caught during June to December tended to be larger (140 to 155 cm AL) with the largest caught in August (Figure 30). Smaller swordfish (100 to 135 cm AL) were caught during January to May, although sample sizes in these months were relatively low. Length-to-age conversion tables revealed that the majority of the sampled catch was immature swordfish 3 to 5 years old.

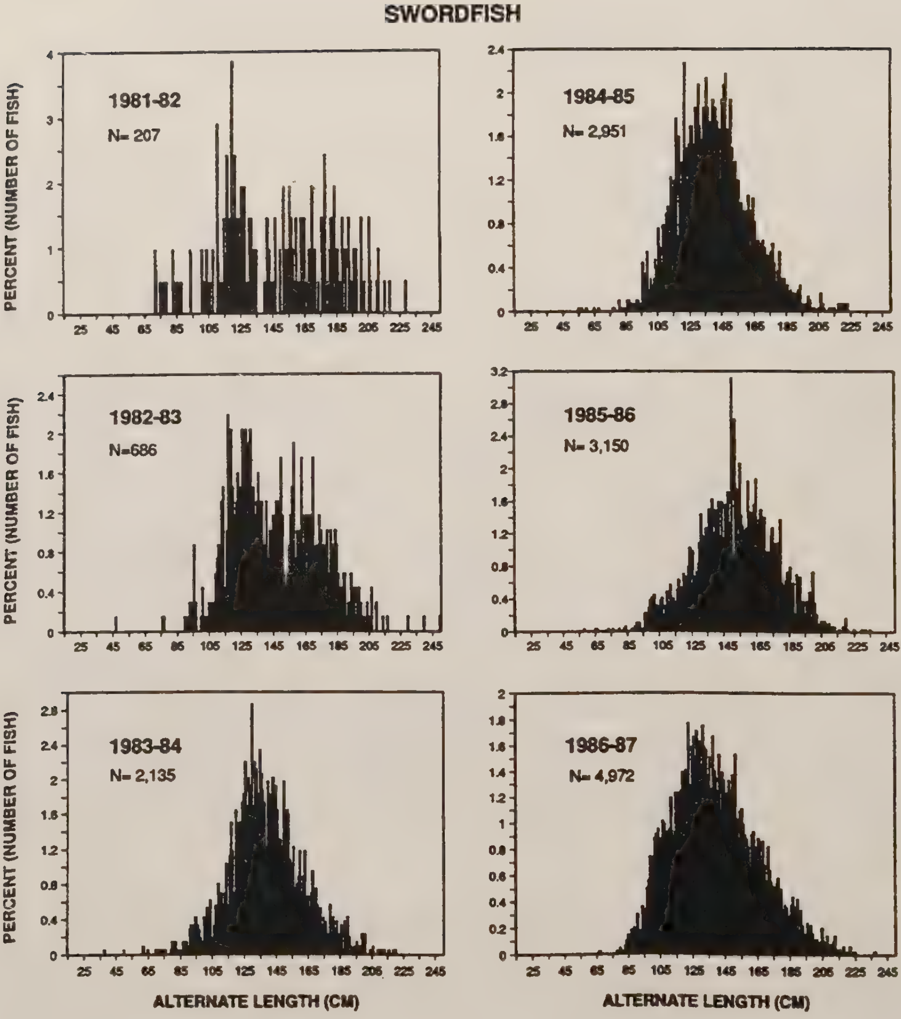


FIGURE 27a. Length-frequency distribution of swordfish sampled at California markets during the 1981-82 through 1986-87 fishing seasons.

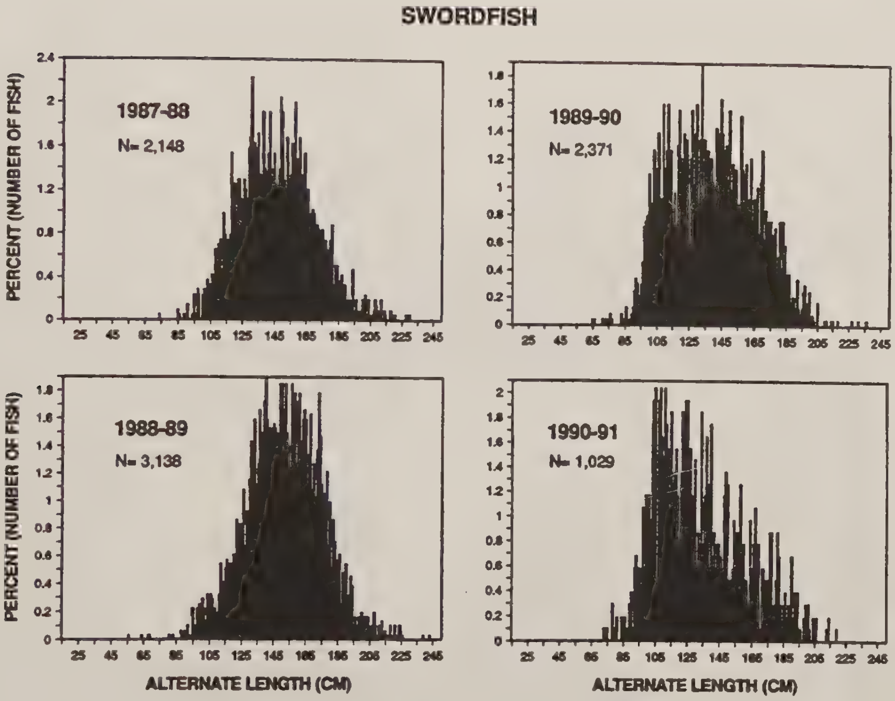


FIGURE 27b. Length-frequency distribution of swordfish sampled at California markets during the 1987-88 through 1990-91 fishing seasons.

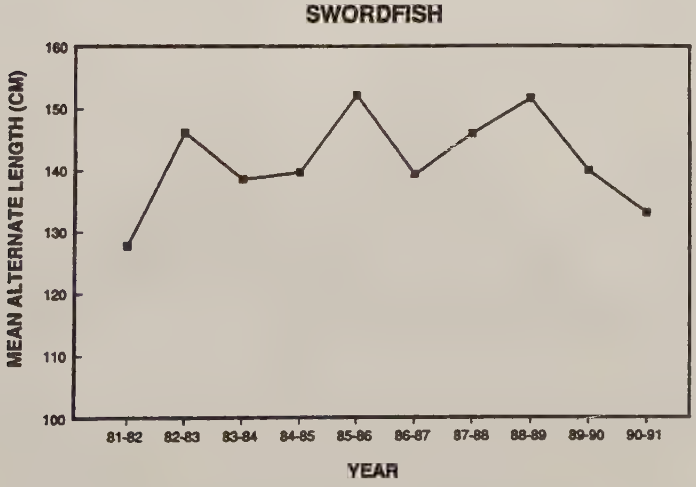


FIGURE 28. Mean alternate length of swordfish sampled at California markets, 1981-82 through 1990-91 fishing seasons.

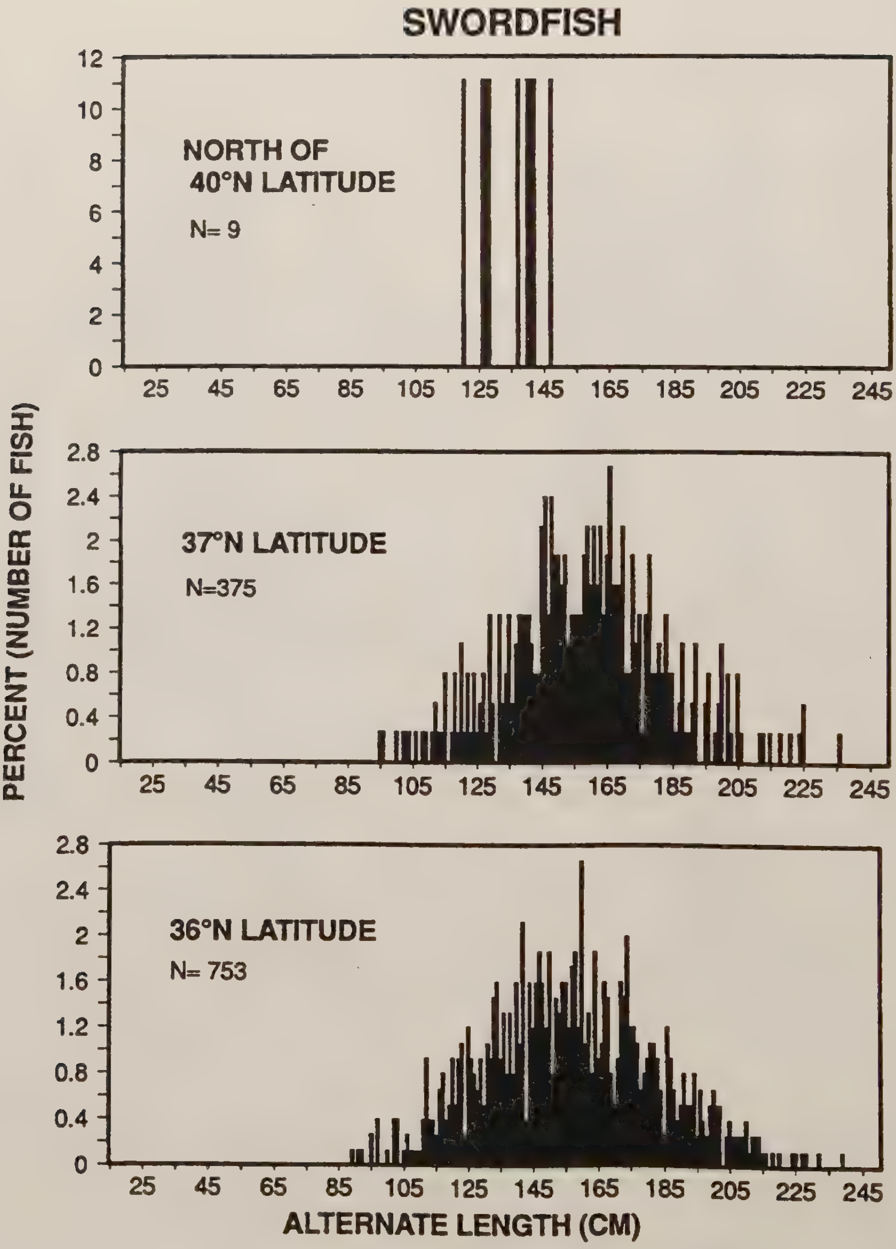


FIGURE 29. Length-frequency distribution of swordfish by latitudinal bands of catch location, from California market samples, 1981-82 through 1990-91 fishing seasons.

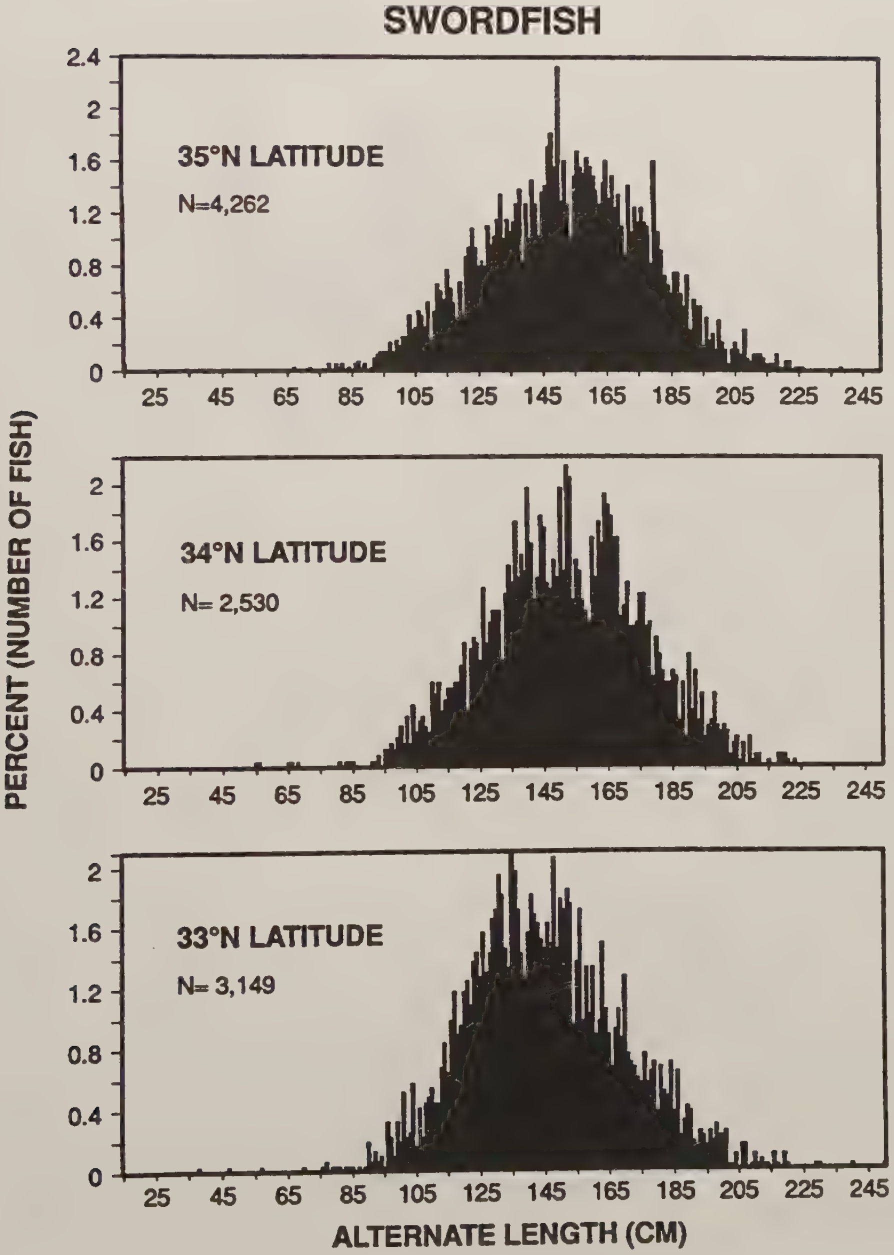


FIGURE 29. (continued)

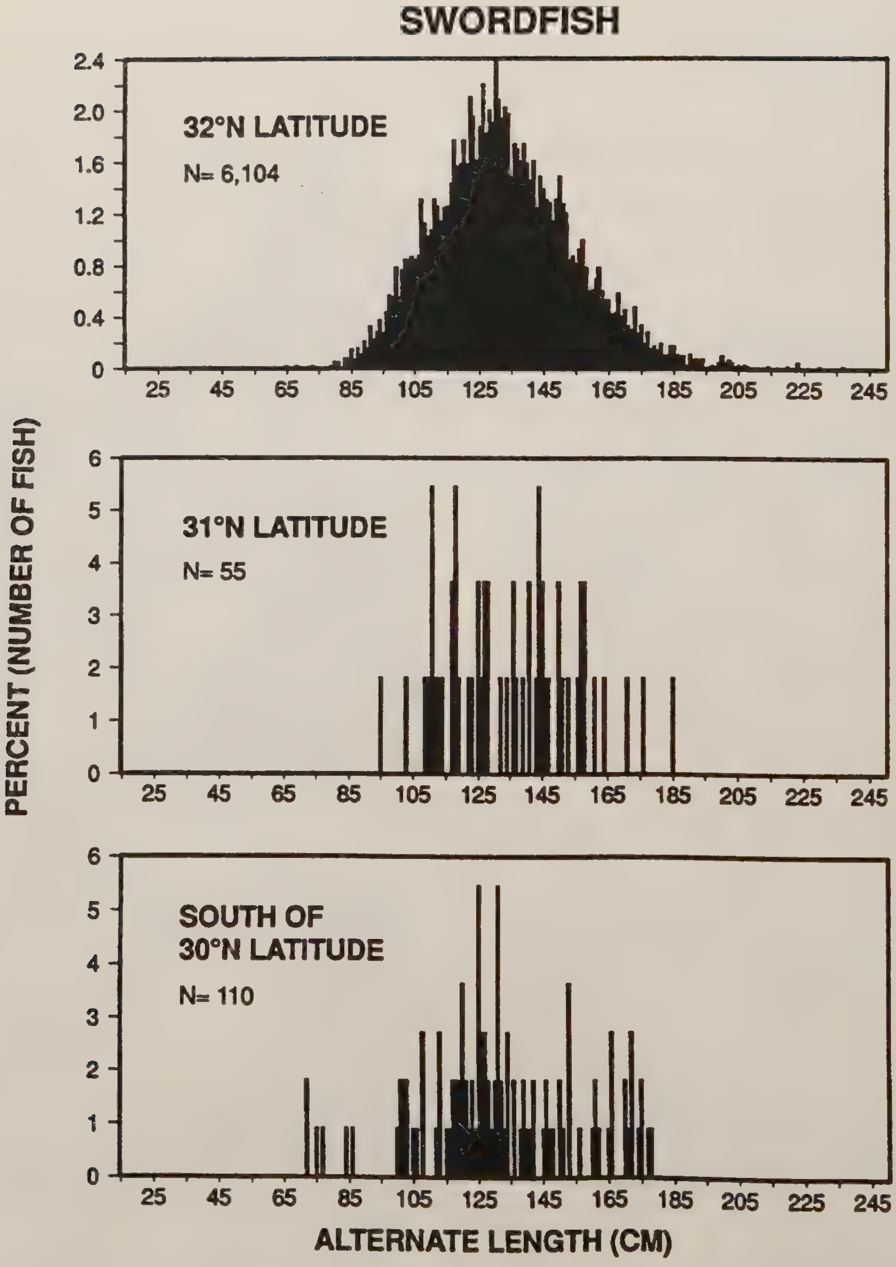


FIGURE 29. (continued)

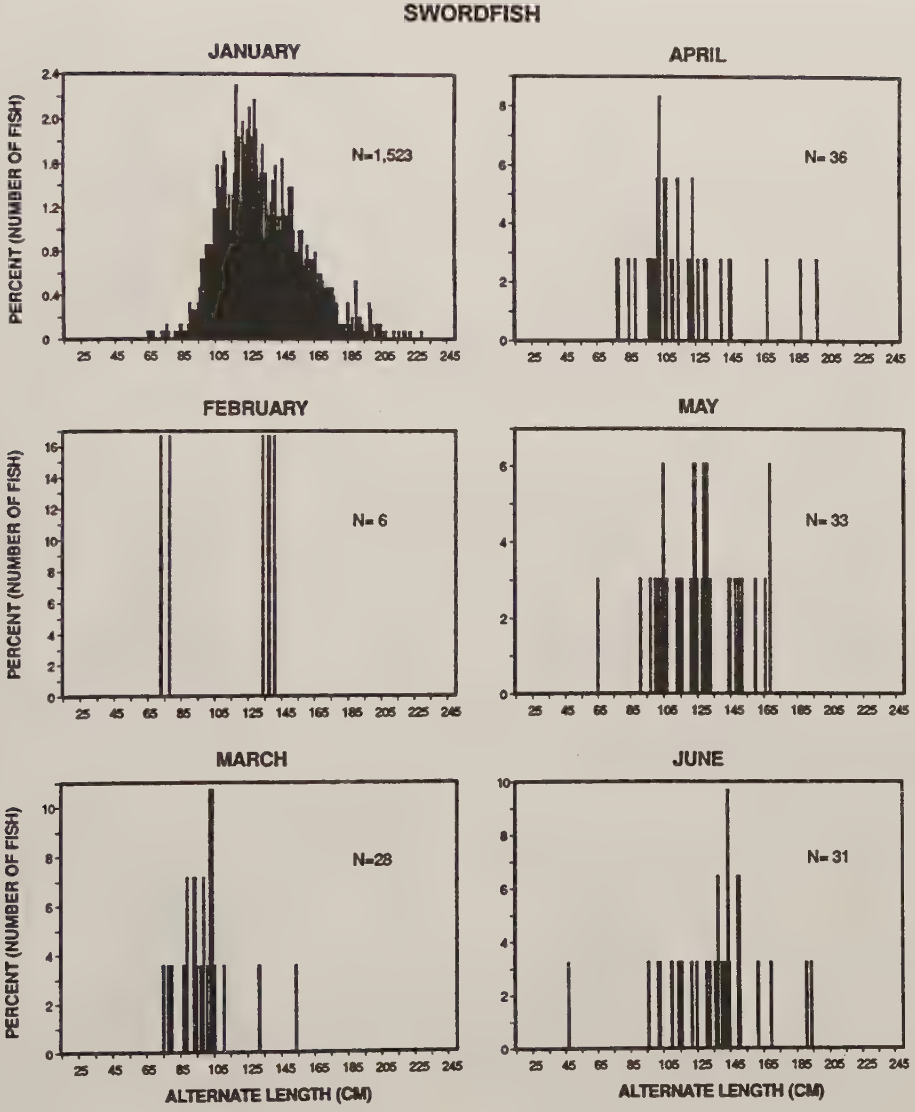


FIGURE 30a. Length-frequency distribution of swordfish by month, January to June, sampled at California markets during the 1981-82 through 1990-91 fishing seasons.

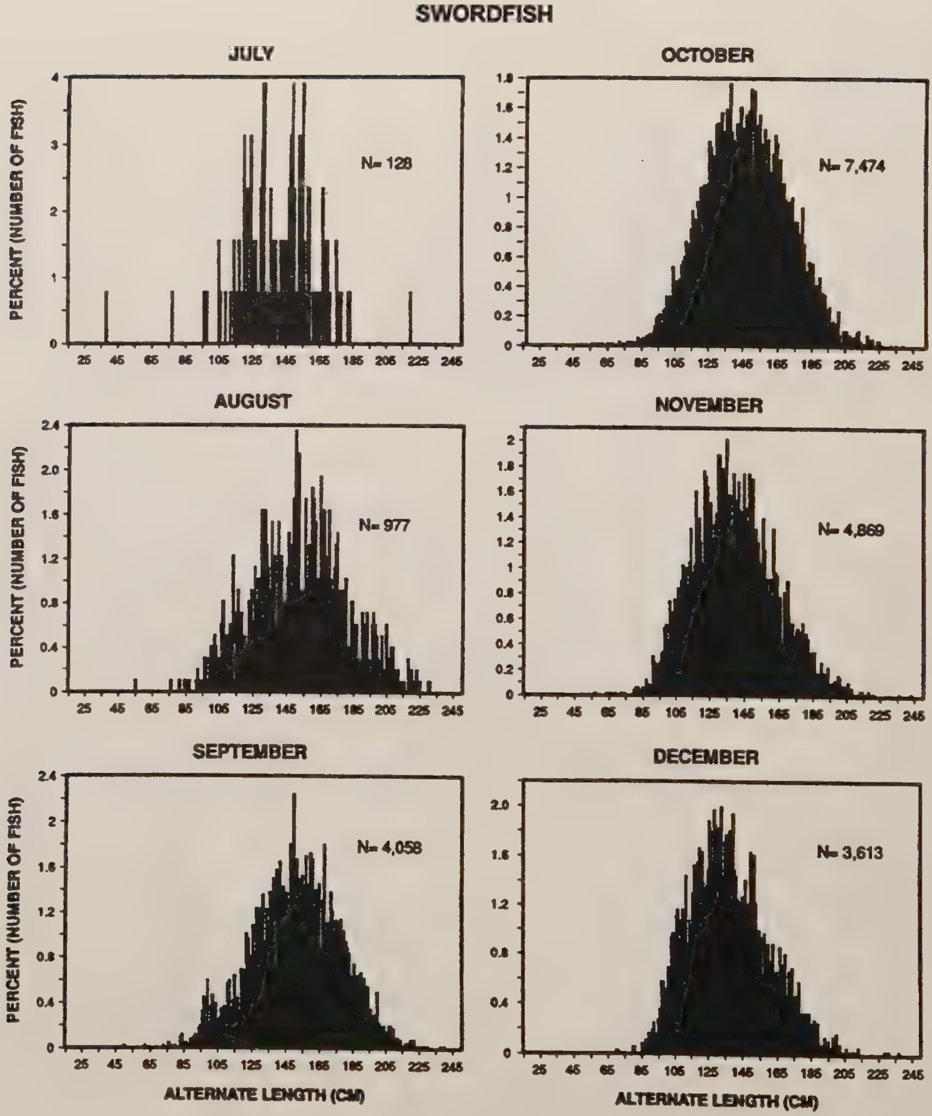


FIGURE 30b. Length-frequency distribution of swordfish by month, July to December, sampled at California markets during the 1981-82 through 1990-91 fishing seasons.

## Common Thresher

During the 10-year period covered, port samplers measured a total of 9646 common threshers ranging from 12 to 136 cm AL with a mean of 60 cm AL (Table 4); most ranged between 40 and 80 cm AL (Figure 31). The alternate length for common thresher represented approximately 17.5 percent of the total length. The means were 65 and 68 cm AL, respectively, for the 1981-82 and 1982-83 seasons, which were fished primarily in the Southern California Bight. The mean length of common threshers peaked in the 1982-83 season at 68 cm AL and steadily declined to a low of 51 cm AL in 1989-90 (Figure 32) even though the drift gill net fishery expanded into previously unfished areas. The size of maturity was estimated at 333 cm TL (56 cm AL) for males and 390 cm TL (75 cm AL) for females (Cailliet and Bedford 1983). Length frequencies indicate that a majority of the catch were immature sharks; mature adults, especially females, represented only a small percentage of the landings during any of the fishing seasons.

As the fishery expanded northward, larger sharks were caught. Common threshers from north of lat. 36°N ranged from 50 to 98 cm AL (Figure 33). In the 1986-87 and 1987-88 seasons off Oregon and Washington, most common threshers caught were adult. A large number of those were males and averaged 76 to 79 cm AL (Stick and Hreha 1988). A small portion (16 individuals) of the Oregon and Washington catch was measured in California and had a mean AL of 75 cm with a range of 63 to 99 cm AL. The range of sizes for common threshers sampled from the lat. 32° to 35°N bands was similar, although those from off San Diego may tend to be somewhat larger (Figure 33). Common threshers caught during July, August, and September tended to be larger (mean AL = 60 cm to 65 cm.; Figure 34). A higher percentage of smaller fish are taken in October, November, and December.

## Pelagic and Bigeye Threshers

Only 116 pelagic and 468 bigeye threshers were measured during the 1981-82 through 1990-91 fishing seasons (Table 4; Figure 35). The small sample sizes are possibly due to misidentifying and recording these species as common threshers. Both species are similar in size to the common thresher and can be difficult to distinguish when cleaned and dressed for market. No trends by season or catch location were apparent for either species.

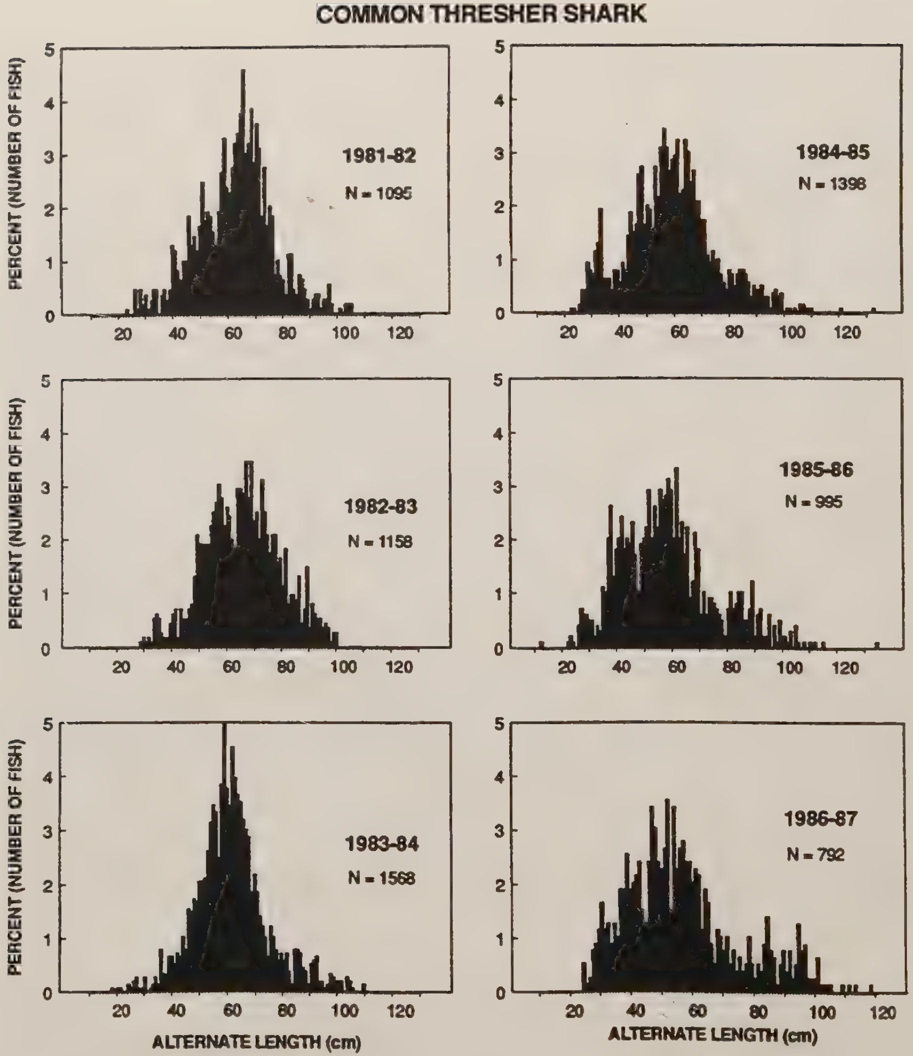


FIGURE 31a. Length-frequency distribution of common thresher sampled at California markets during the 1981-82 through 1986-87 fishing seasons.

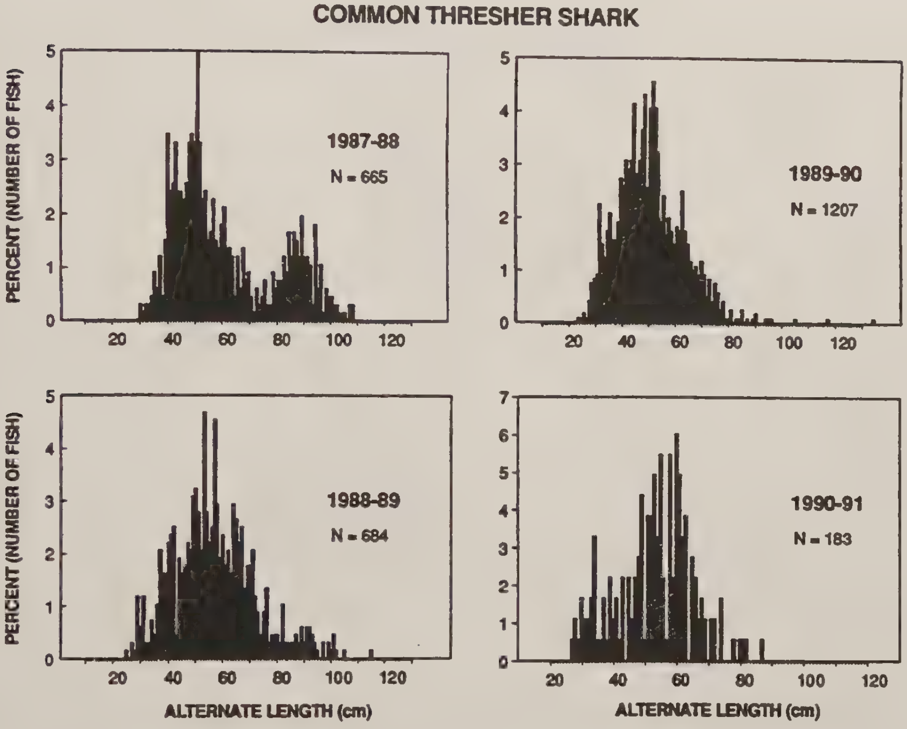


FIGURE 31b. Length-frequency distrbution of common thresher sampled at California markets during the 1987-88 through 1990-91 fishing seasons.

## Shortfin Mako

A total of 5659 shortfin makos were sampled by the CDFG during 1981-82 through 1990-91. Length measurements ranged from 6 to 134 cm AL (Table 4; Figure 36) with a mean of 47 cm AL. Reported lengths of fish less than 20 cm are suspect and are probably erroneous measurements. The mean length declined from 58 cm AL in 1982-83 to less than 35 cm AL in 1985-86, then averaged about 47 cm AL over the next 5 years (Figure 37). Length distributions for the 1982-83 and 1985-86 seasons may unrepresentative due to the small sample sizes and limited area (south of Point Conception) and season (late October and early November) of coverage.

There was a trend towards larger shortfin makos in the northern areas (Figure 38). Shortfin makos caught south of San Diego (the lat. 32°N band and south) had a mean AL length of 43 cm, while those off San Diego and Los Angeles had

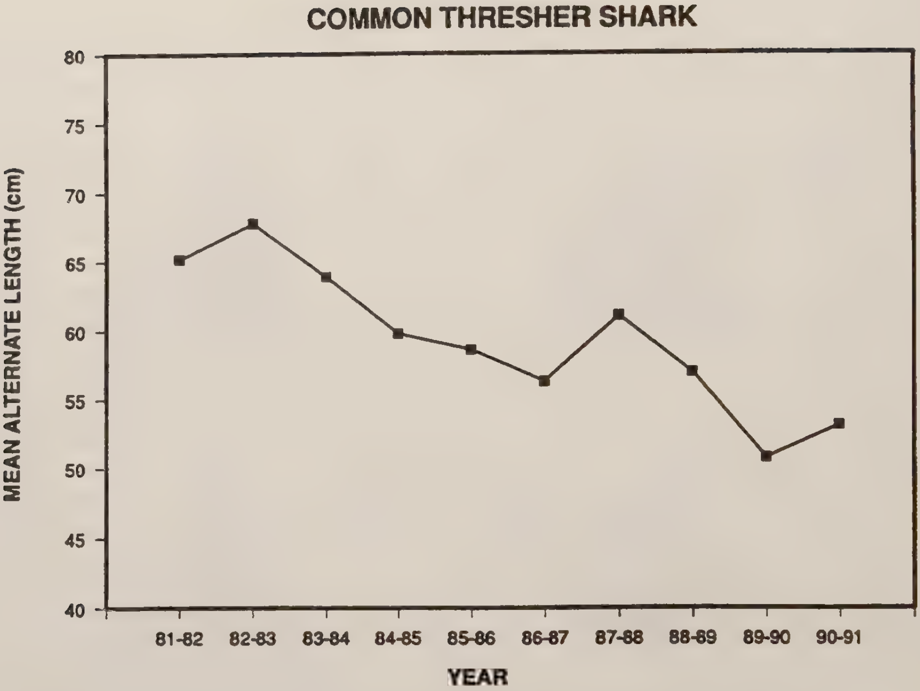


FIGURE 32. Mean alternate length of common thresher sampled at California markets, 1981-82 through 1990-91 fishing seasons.

a mean AL length of 49 cm. Shortfin makos sampled from the lat. 35° and 36°N bands (San Luis Obispo to Santa Cruz) had annual AL means ranging from 52 to 55 cm. Shortfin makos caught during May through August tended to be larger than those caught during October through December (Figure 39).

Alternate length of the shortfin mako shark represents about 34% of total body length. Because males mature at 195 cm TL (66 cm AL) and females mature at 280 cm TL (95 cm AL; Stevens 1983), it is clear that the catch was composed almost entirely of juveniles.

## Opah

During the period covered, 1967 opahs were measured and sizes ranged from 10 to 242 cm FL (Table 4; Figure 40). The majority of the lengths were centered in three modes at 80, 100, and 112 cm FL. Due to the small number of opahs measured, any difference between sizes of fish caught in the north and south were not evident.

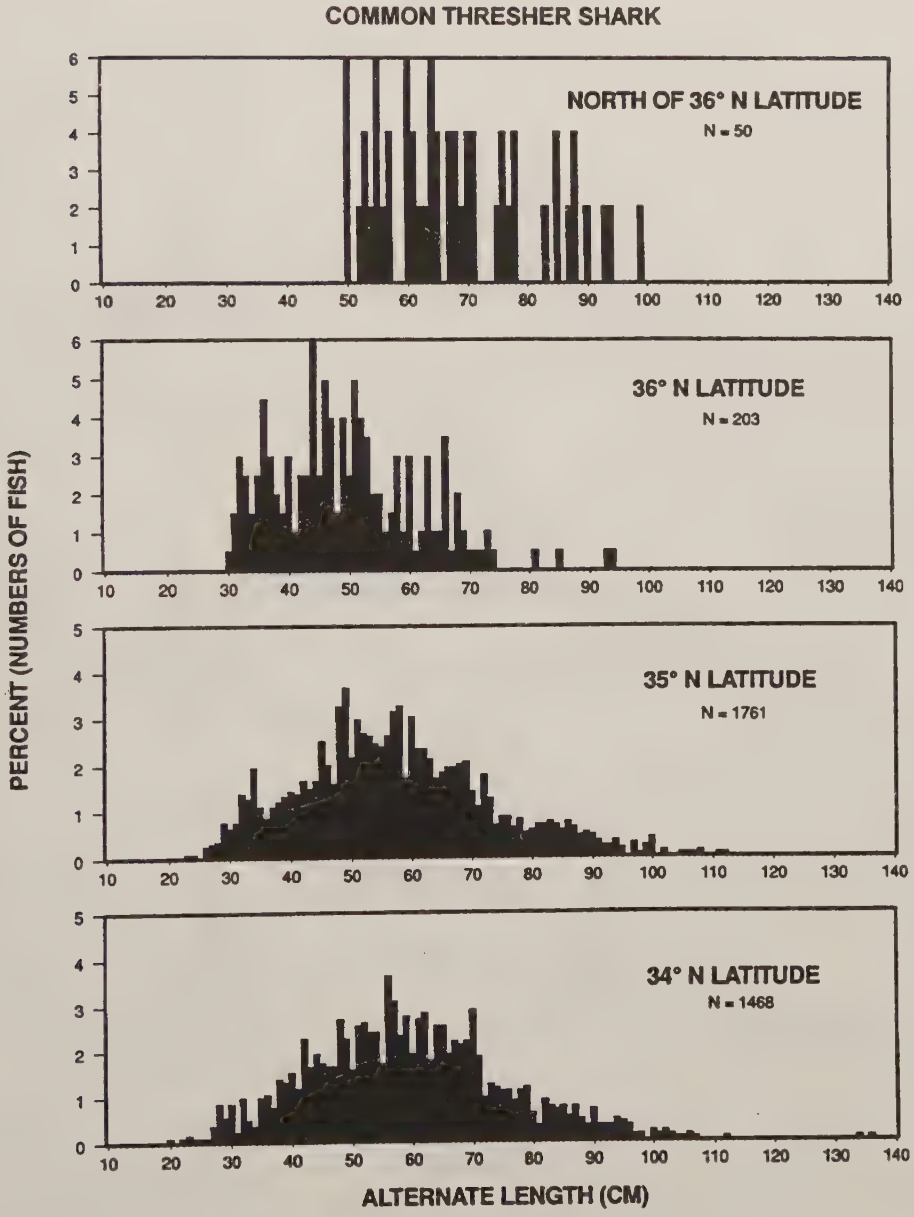


FIGURE 33. Length-frequency distribution of common thresher by latitudial bands of catch location, from California market samples, 1981-82 through 1990-91 fishing seasons.

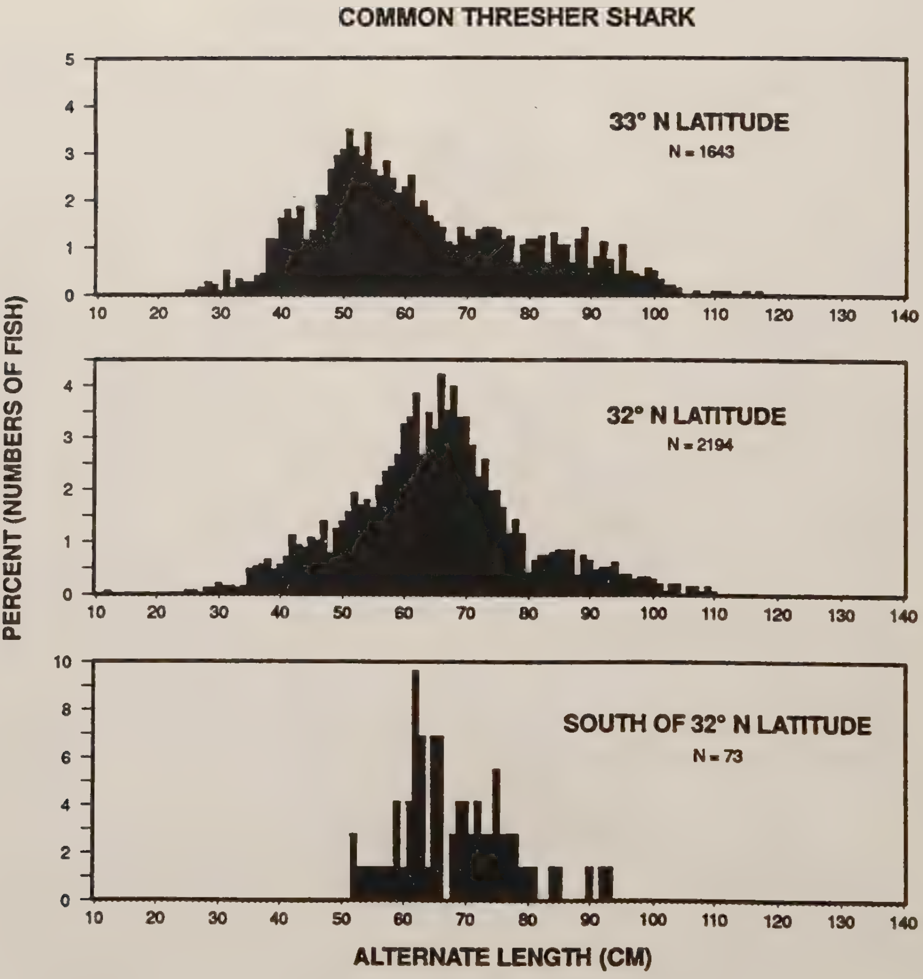


FIGURE 33. (continued)

# DISCUSSION

We have presented a description of the California drift gill net fishery, which evolved from a small nearshore experiment to a major California fishery. There have been major changes in nearly every aspect of the fishery including boats, gear, fishing techniques, regulations, fishing areas, seasons, and targeted species. We are particularly pleased with the manner in which we were able to incorporate both landing receipt and logbook data along with market samples to

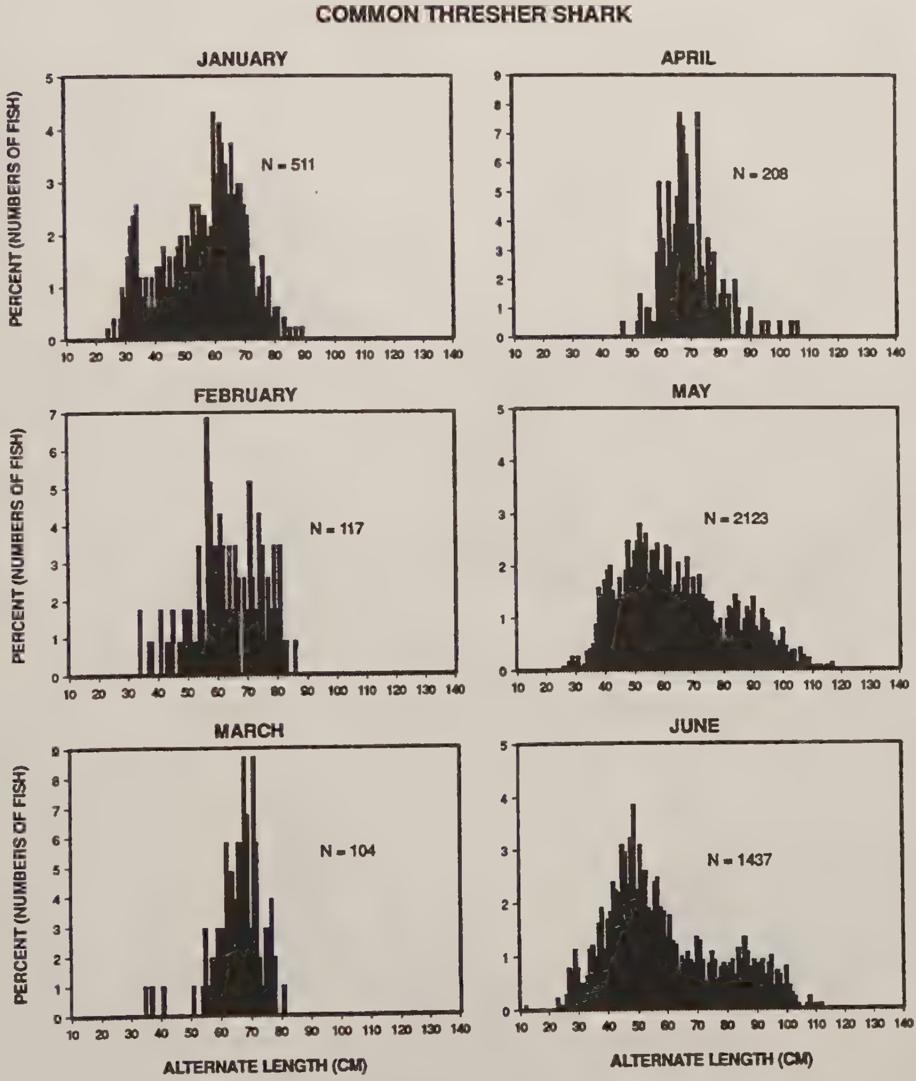


FIGURE 34a. Length-frequency distibution of common thresher by month, January to June, sampled at California markets during the 1981-82 through 1990-91 fishing seasons.

summarize important facets of the fishery. We encourage others to utilize these sources for further, more in-depth analyses of this fishery and related stocks.

We feel that the quality of all data collected for the drift gill net fishery, while relatively high in some areas, can be improved. We found some confusion in the way logbooks were completed, especially in the recording of catch. In some cases,

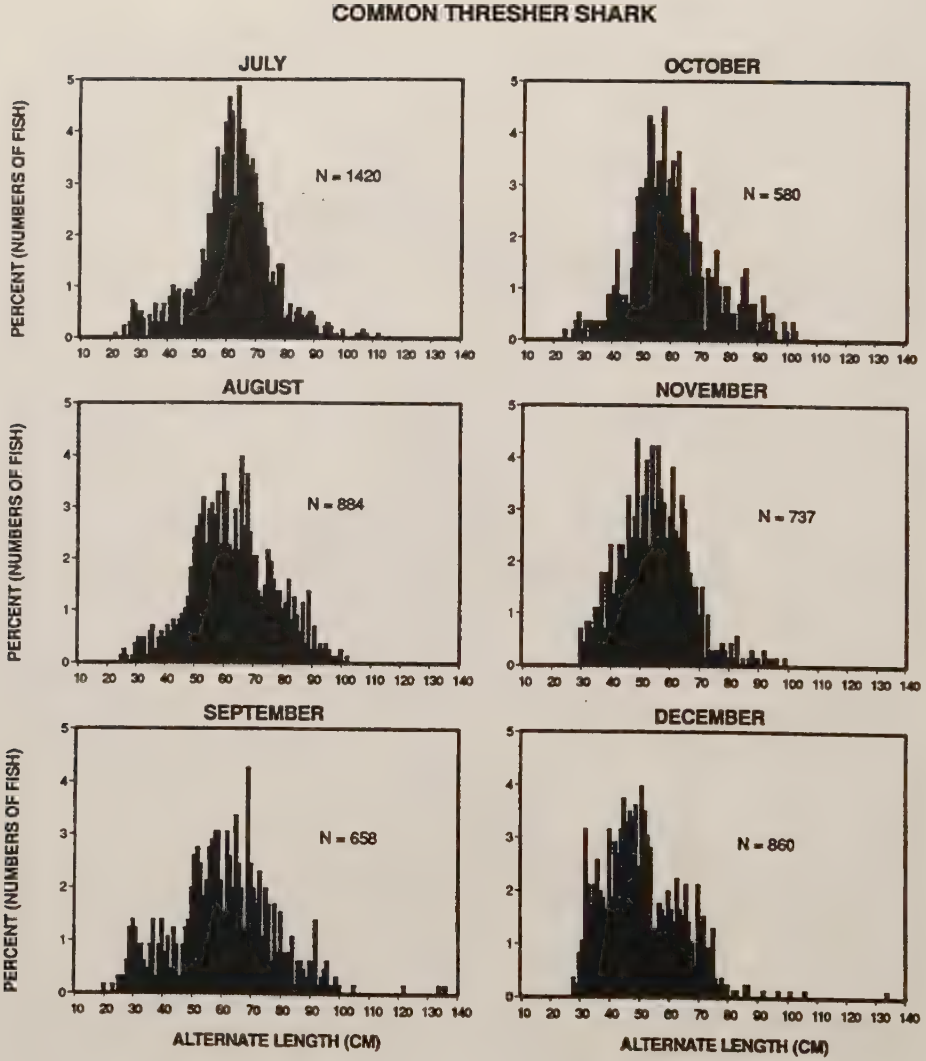
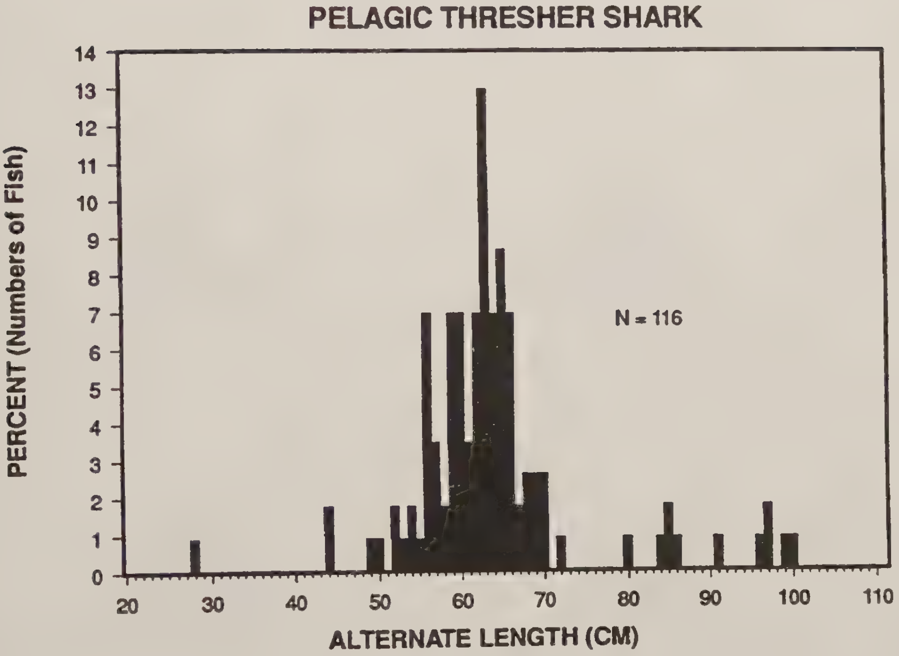


FIGURE 34b. Length-frequency distribution of common thresher by month, July to December, sampled at California markets during the 1981-82 through 1990-91 fishing seasons.

catch was reported by number, in other cases by weight, and many times without any indication of which units were used or if a combination of both was used. Much of this confusion could be eliminated if more complete instructions were provided with the logbooks. There was also some intentional misrepresentation such as miscoding of gear types on landing receipts and net-caught swordfish



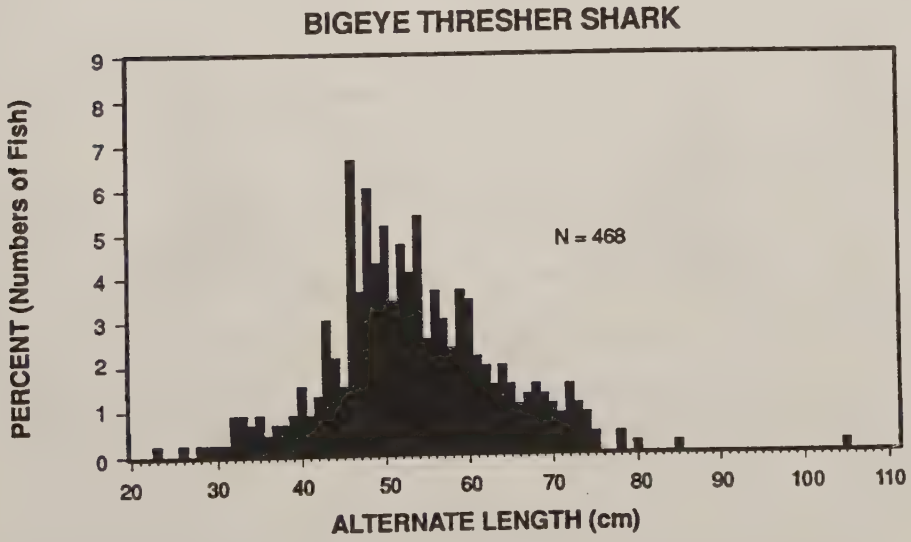


FIGURE 35. Length-frequency distribution of pelagic thresher and bigeye thresher sampled at California markets during the 1981-82 through 1990-91 fishing seasons.

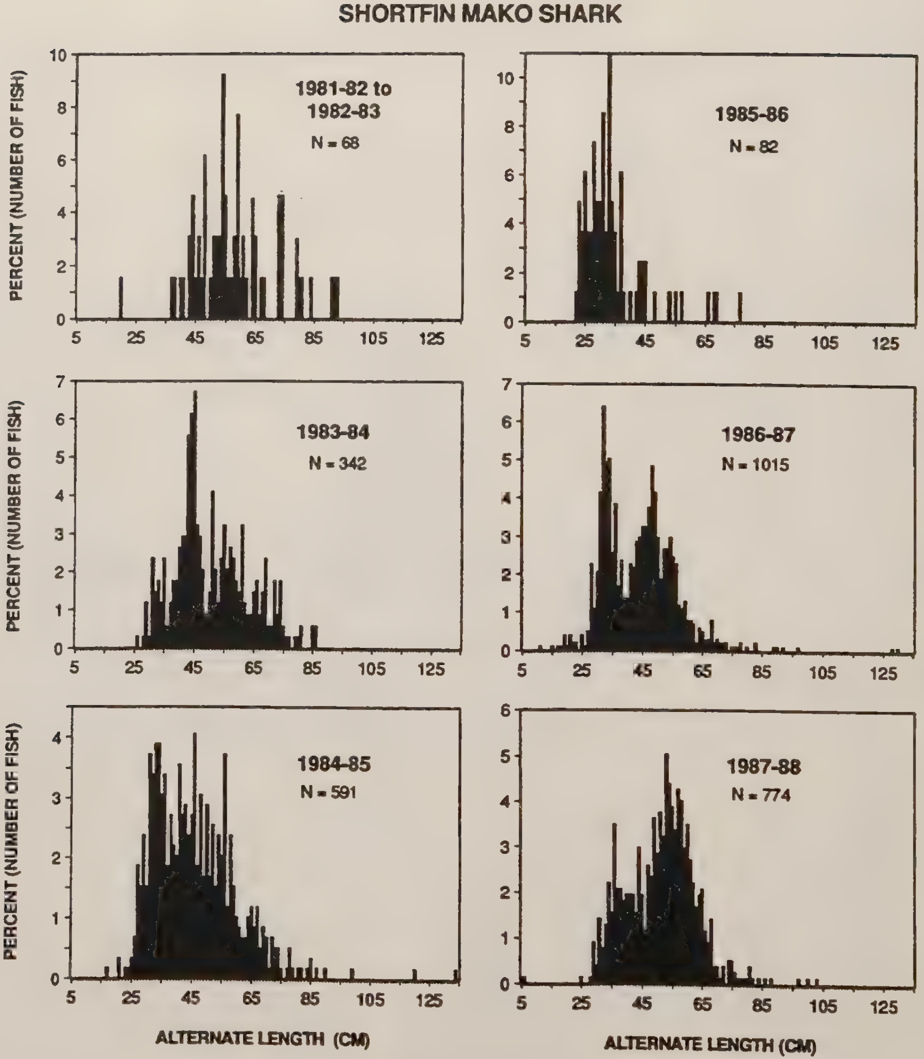


FIGURE 36a. Length-frequency distribution of shortfin mako sampled at California markets during the 1981-82 through 1987-88 fishing seasons.

stuck with a harpoon after capture (especially during the period when swordfish landings from drift gill net gear were not allowed to exceed shark landings).

Coverage rates of the market sampling system for sizes of fish are comparable to other fishery sampling programs. However, the adequacy of this level of sampling is difficult to assess since no formal sampling plan exists. The quality of

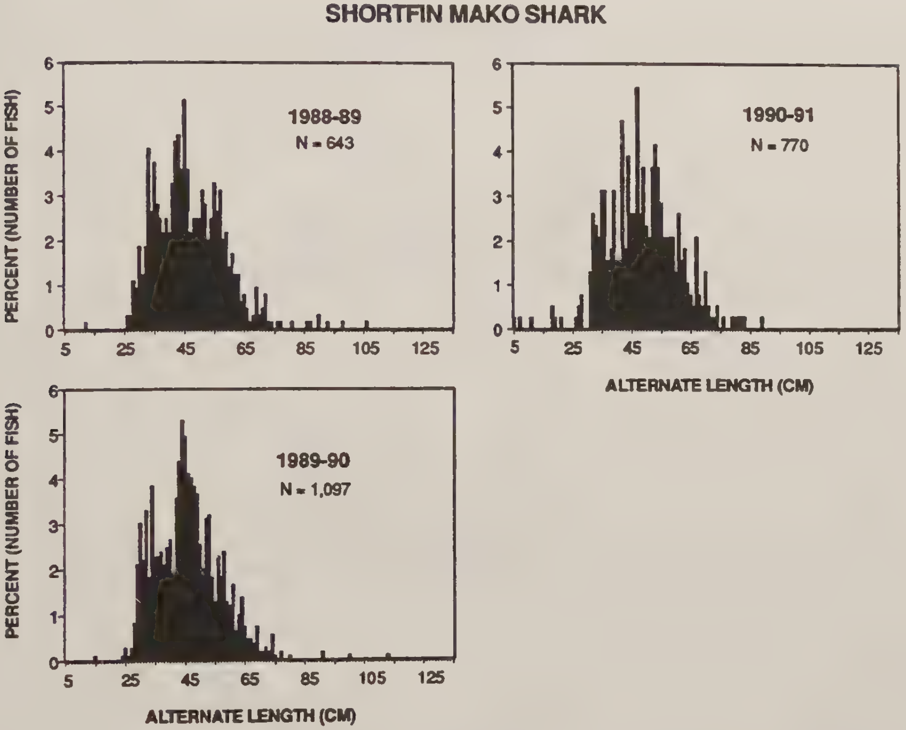


FIGURE 36b. Length-frequency distribution of shortfin mako sampled at California markets during the 1988-89 through 1990-1991 fishing seasons.

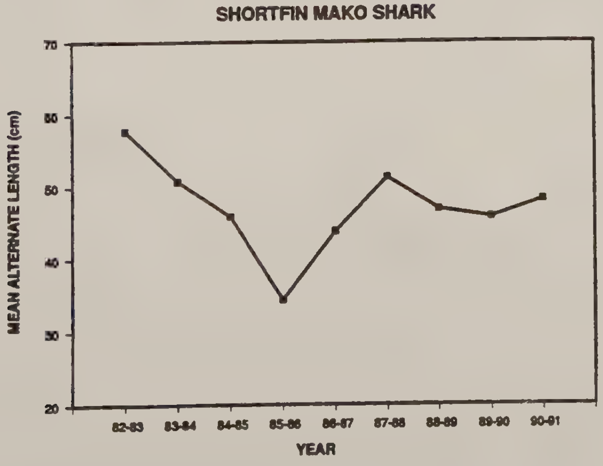


FIGURE 37. Mean alternate length of shortfin mako sampled at California markets, 1982-83 through 1990-91 fishing seasons.

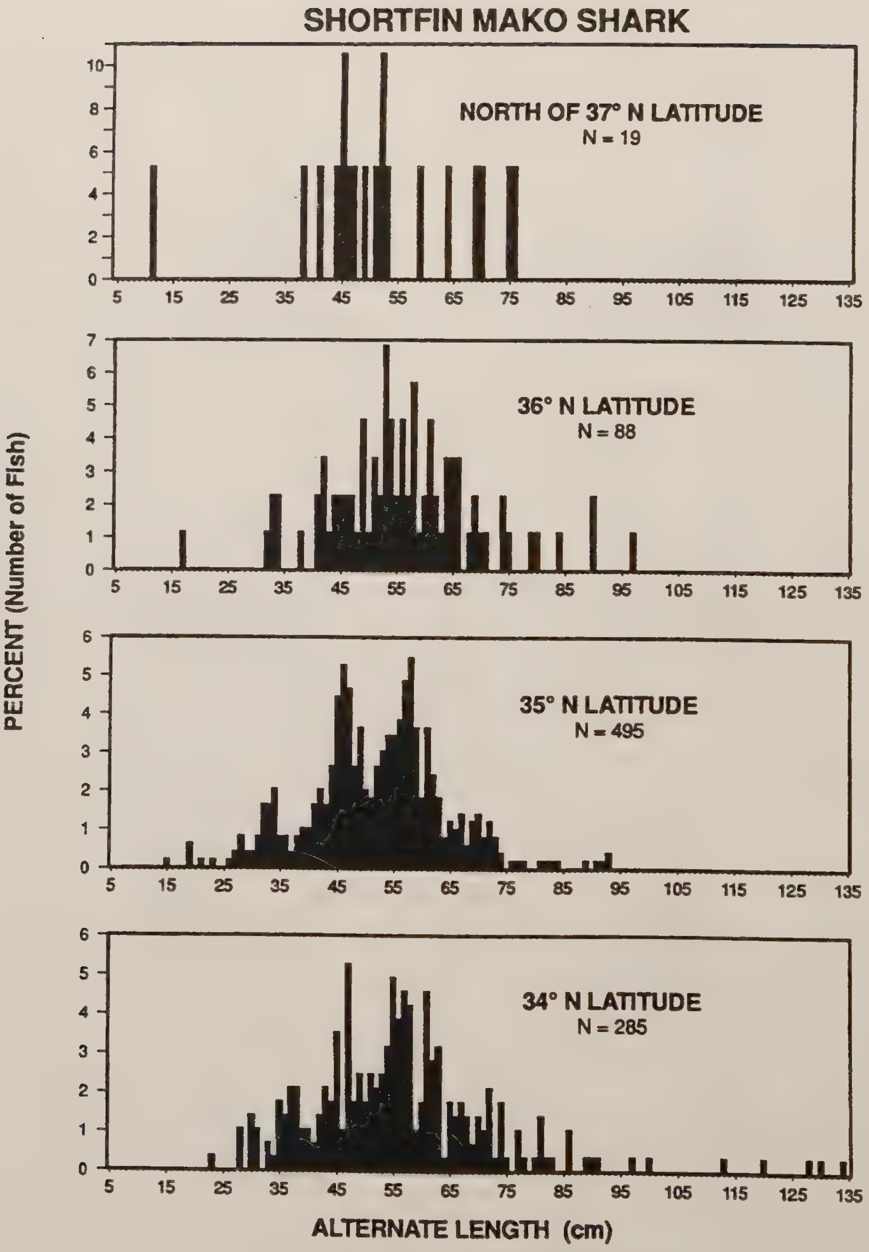


FIGURE 38. Length-frequency distribution of shortfin mako by latitudinal bands of catch location, from California market samples, 1981-82 through 1990-91 fishing seasons.

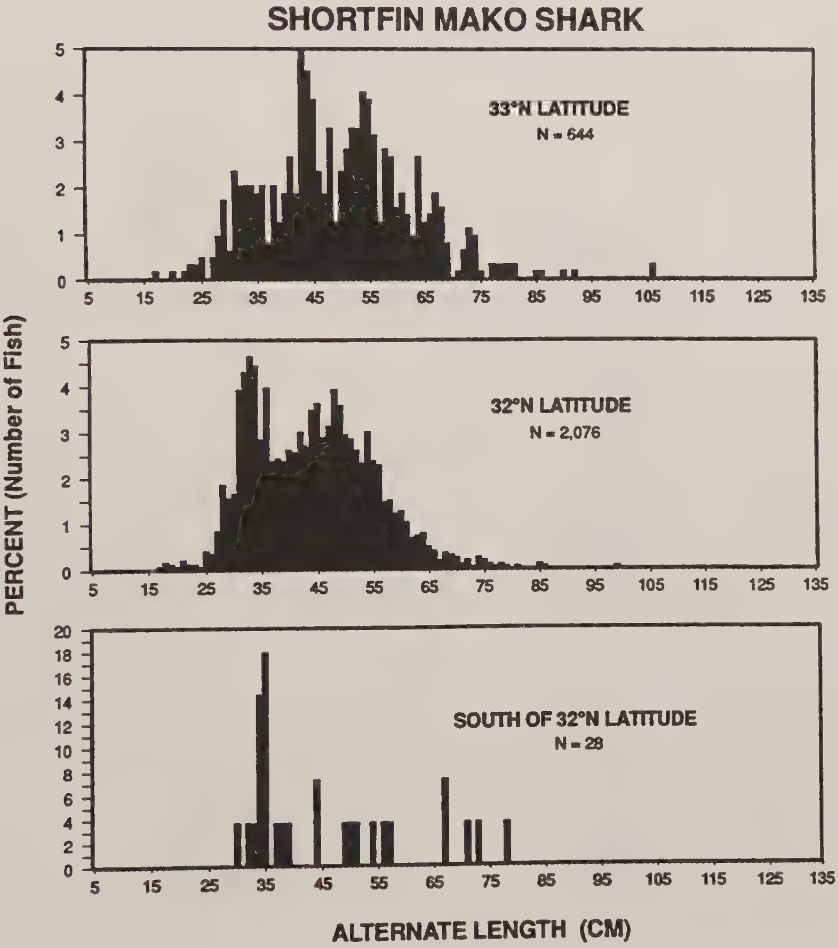


FIGURE 38. (continued)

length data may be improved by the establishment of a formal sampling plan which would evaluate sample sizes by species and month of landing.

We made major assumptions to separate landings between set gill net and drift gill net gear, because many landing receipts did not distinguish between the two nets and reported gear type only as gill net. These assumptions may have biased estimates of landings for some species and may have biased estimates for number of vessels using drift gill nets. While we feel that these biases are relatively low, a revision of landing receipts to allow for separate entries for drift and set gill nets as well as instructions explaining the problems in separating these catches

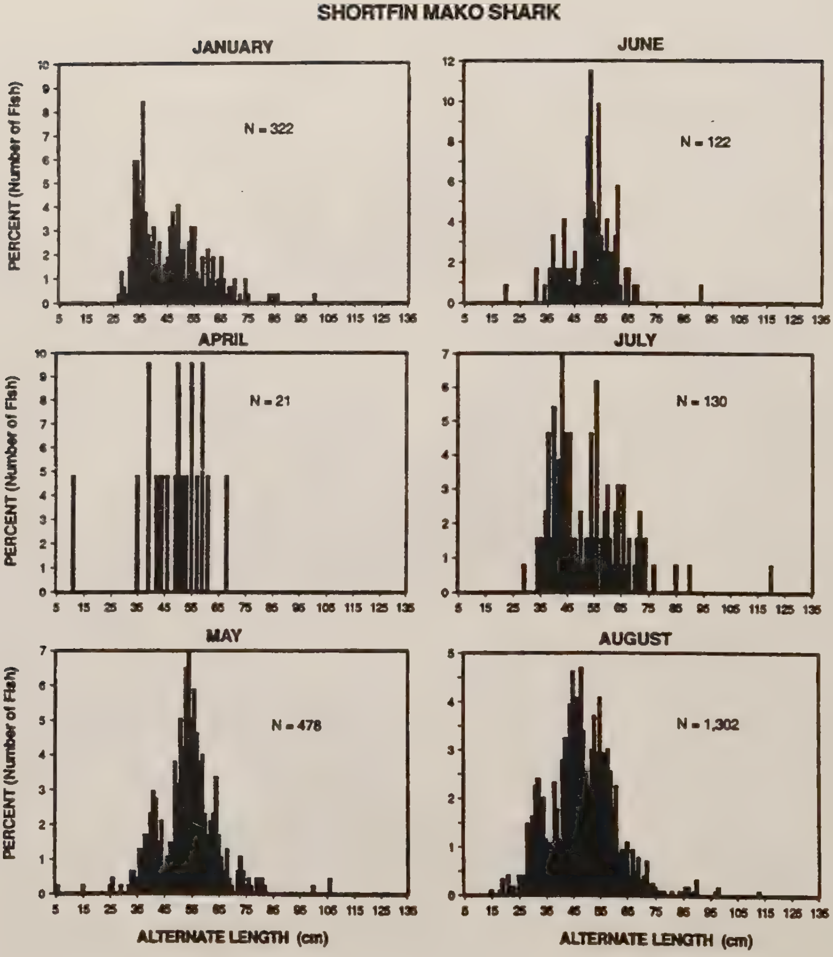


FIGURE 39a. Length-frequency distribution of shortfin mako by month, January to August, sampled at California markets, 1981-82 through 1990-91 fishing seasons.

and soliciting compliance in accurately entering the gear type would eliminate the need for many of these assumptions and increase the quality of the landings data.

This study summarizes the pertinent available data obtained from the California logbook system, landing receipts, and market sampling. These data form a base line from which changes in the fishery and harvested stocks can be com-

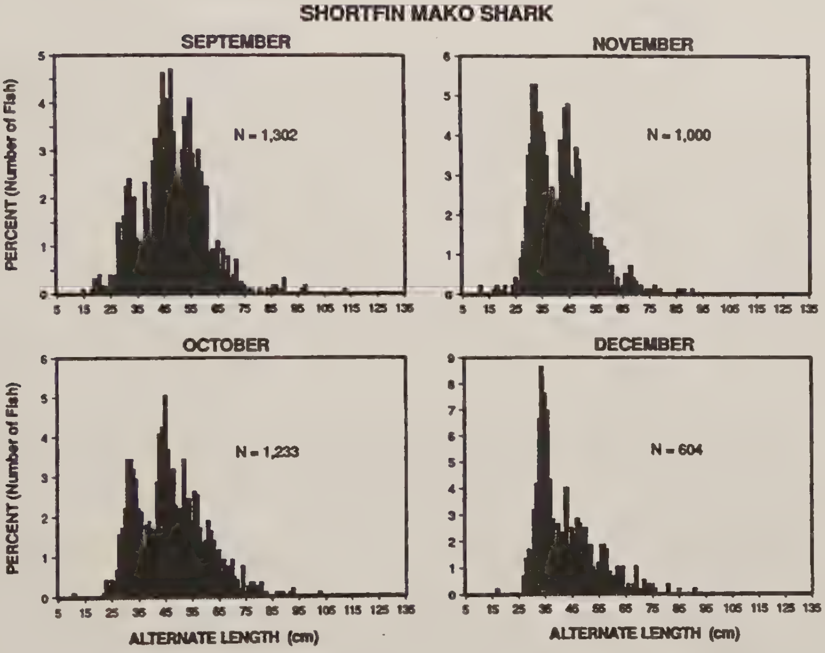


FIGURE 39b. Length-frequency distribution of shortfin mako by month, September to December, sampled at California markets, 1981-82 through 1990-91 fishing seasons.

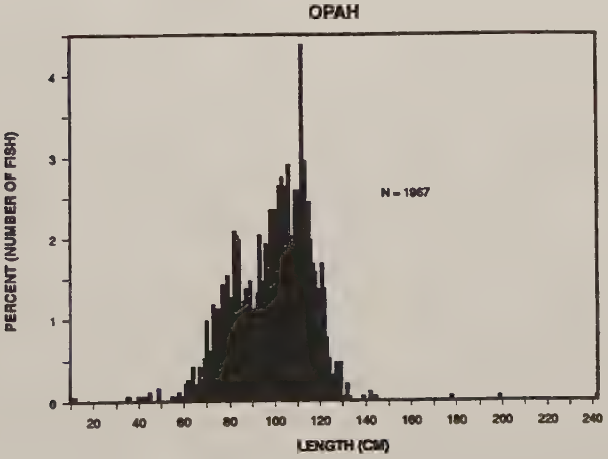


FIGURE 40. Length-frequency distribution of opah sampled at California markets, 1981-82 through 1990-91 fishing seasons.

pared in the future. More detailed analyses of trends in the fishery and the resources should follow.

We have shown that the California drift gill net fishery operated primarily in the area between San Diego and Cape Mendocino, concentrating on swordfish in the Southern California Bight during the months of May to December.

Since the 1985-86 fishing season, fishing effort has decreased 50% to 60% and the decreasing effort corresponds to decreasing total landings of the same proportions. Both decreases are due in part to the spring fishing closure for sharks. Decreases in landings of common thresher were over 80%, while swordfish and shortfin mako landings decreased 60% and 40%, respectively. Sizes of swordfish showed no increasing or decreasing trend. Mean sizes of common thresher decreased 21% from the 1982-83 season to less than 55 cm AL in the 1990-91 season. There was no significant change in the mean size of shortfin mako, although a small sample size in 1982-83 and nonrepresentative sample in 1985-86 were responsible for a seeming decrease during the period we examined (Figure 37).

The decreases in landings can be directly related to decreased fishing effort. However, the corresponding decreases in mean size of common thresher may indicate a problem within this population or that the fishery does not operate at the times or in the areas when big fish are present. We therefore recommend that further investigations including catch per unit effort be conducted for the major species caught by this fishery.

There have been a number of problems and conflicts that have occurred during the first 10 years of the fishery (e.g. sea lion, gray whale, and marlin bycatch). These have been addressed and resolved interactively through the cooperative efforts of the commercial industry, the recreational fishing industry, environmental groups, and State and Federal governments. These efforts, which included many specific, problem-oriented time and area restrictions, resulted in an overall reduction in fishing intensity and the bycatch of marine mammals.

Concerns regarding the drift gill net fishery are similar to those expressed when the fishery started. Specifically, shark fisheries throughout the world historically have not been sustained and in fact, tend to decline significantly or crash rather suddenly (Compagno 1990). Shortfin makos and common threshers taken by the California drift gill net fishery within the Southern California Bight are primarily juveniles. In response to declines in the quantity and size of common thresher caught, the State virtually eliminated the directed fishery with area and season closures. If the number and size of shortfin makos caught should also decline, similar management controls may be warranted.

In the early 1980s, the incidental catch of marine mammals was relatively high, but time and area closures around the Channel Islands and along the mainland apparently were successful in reducing that catch. Currently, the incidental catch of marine mammals in this fishery is apparently not compromising any stocks, but the potential for a significant bycatch remains and may involve some species listed under the Endangered Species Act. Thus, continued monitoring, as with the NMFS mandatory observer program, is prudent.

Bycatch of fish does not appear to be a problem except possibly for blue sharks which are caught but not utilized. As this catch is not reported or monitored, it might also be a significant problem in determining the status of local populations. Important changes in abundance may not be detected in time to make prudent management decisions. Because fishing mortality and stock status of blue shark are unknown, close monitoring of the commercial as well as recreational fisheries is warranted.

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# An Overview of Guam's Inshore Fisheries

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*ABSTRACT—Guam's nearshore reef fishery is a multi-gear, multispecies fishery that has undergone major changes through the years. Methods have evolved and become more modern. This, along with the changing economic status of Guam, has severely stressed the fishery. Top targeted species are being overexploited and "growth overharvesting" is occurring; the more serious form of "recruitment overharvesting," is happening to some of the key species. Major management concerns are discussed with respect to overfishing and habitat destruction. Management recommendations for this fishery include gear restrictions, size restrictions, and the establishment of marine conservation areas.*

## Introduction

### Background

Since long before the first contact of westerners with native Guamanians (or Chamorus[1]) in 1521, fish has been the primary source of protein for the islanders. Little is known about traditional management of Guam's fisheries, but fishing was and has remained an important part of life and culture. In the past, subsistence fishing provided Guam's residents with an ample supply of fish. Most of the fish caught were consumed by fishermen's families or shared with the community and were harvested from three main areas of the sea: The coral or nearshore shallow adjacent areas, nearshore slopes to about 100 fathoms and the surface ocean waters. Much of the traditional use of fish for social obligations in the form of fiestas (large gatherings for funerals, weddings, christenings) is still practiced.

Guam is a U.S. territory located in the western Pacific (Fig. 1). It is the southernmost and largest island in the Mariana Island Archipelago with over 130,000 people on about 550 km$^2$. Much of the change in Guam's fisheries, from traditional subsistence fisheries to the more modern subsistence, commercial, and recreational fisheries has occurred since World War II. Johannes (1978) maintained that the decline of the Pacific island fisheries was due mostly to change in the economic system of the Pacific Islands to a more western one which has eroded the ancient marine tenure laws and tra-

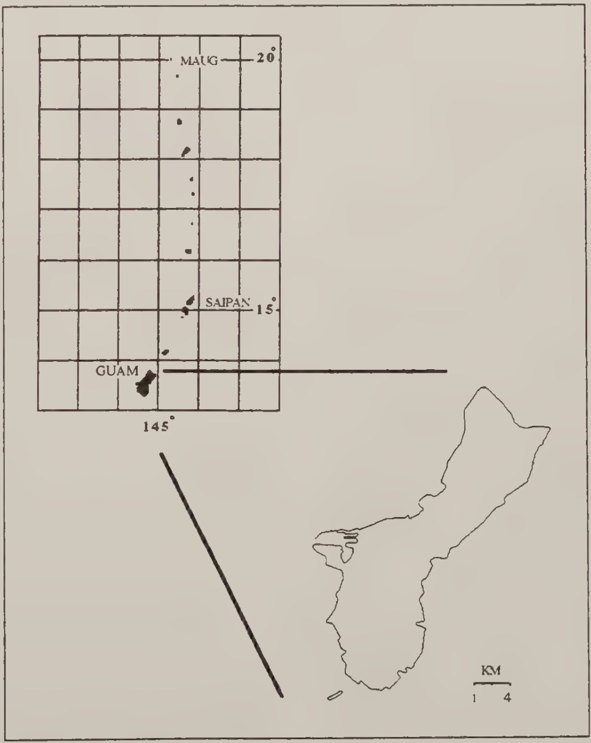

Figure 1.—Guam (13°30'N; 144°50'E) is the southernmost of the Mariana Archipelago.

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[1] Chamoru, previously Chamorro, is the currently accepted spelling of the indigenous people of Guam.

ditional island conservation ethics. This, along with the introduction of more modern, manufactured fishing materials (monofilament nets, steel hooks, poles, reels, spearguns, scuba gear, etc.), has changed the complexion of Guam's inshore fishery and aided in the decline of the nearshore reef fishery. Ikehara et al. (1970) stated that Guam's shallow inner reefs appeared to be fully exploited and showed signs of overfishing. Katnik (1982) found that two heavily fished areas on Guam were overfished and stated that other accessible areas on Guam could be equally overexploited. What was once a well stocked, complex fishery with diverse fishing methods has changed to a fishery under serious fishing pressure.

### Scope

Because of the increased efficiency of fishing techniques due to introduction of modern materials and because of the increase in fishermen and the island population, the Guam Division of Aquatic and Wildlife Resources (DAWR) recognized the need to protect the fishery from overharvesting. Initial monitoring of the resources began in the 1960's, and it had evolved by 1982 into the current creel survey methodology adapted from Malvestuto et al. (1978). Because of the different usage and the different areas of the sea utilized for the multispecies, multigear fisheries, Guam's fisheries monitoring was divided into two projects. These were the "inshore" (or nearshore reef ) fisheries and the "offshore" (small boat) fisheries (Myers, 1993). The inshore fisheries discussed here will encompass the coral or nearshore shallow adjacent waters which consists mostly of fringe reefs.

This paper describes inshore fisheries, concentrating on data from 1982 through 1991. We discuss fishing techniques and data collection and compilation for landing and effort estimates of Guam's fishery. The harvest components (finfish, nonfinfish, and seasonal juveniles or traditional fishery) and current management practices are described with suggestions for conservation of the fishery.

## Guam's Inshore Fisheries

### Historic Fishing Methods

Detailed fishing techniques from prehistoric times have been described by Amesbury et al. (1986) and will be only briefly described here. Early fishing techniques (prior to the 1930–40 period) employed gear composed of natural materials. Today, inshore (or reef and lagoon) methods have incorporated modern equipment and have been modified in some manner from the traditional form of fishing. Some form of hook and line fishing, usually handline, has been done since the arrival of the Chamorus on Guam around 1500 BC (Amesbury et al., 1986). Net fishing has included forms of dip netting, bag seining, throw netting, surround netting, drag netting, and gill netting (a more recent form of net fishing). Fishing with traps and spears has occurred throughout the history of Guam. Women historically harvested the seagrass parrotfish (Scaridae) and some wrasses (Labridae) by hand. All social classes of Chamorus harvested eels with iron spears and crabs with multipronged spears. Gleaning for invertebrates has always occurred, especially for mollusks and algae for use as either bait or food. The Spaniards gleaned for sea cucumbers.

Several types of fishing no longer occur. Two of these are the opelu or hachuman fishing (for *Decapterus* sp.) and the decoy method of fishing (Amesbury et al., 1986). Turtles were harvested until 1976 when it was prohibited. Other currently prohibited methods include fish weirs, fish poisoning from root extract (*Barringtonia asiatica* tree), chlorine bleaching, and dynamiting. These are still practiced illegally on a small scale.

Traditional fishing practices are still observed routinely on Guam. One practice is the fishing for seasonal juveniles recruiting to the reef flats (discussed below), while the other practice involves sharing the catch. The catch from the surround net or chenchulu (when used for catching seasonal mackerel or *Selar crumenopthalmus*) is still divided up into thirds with the portions going to the owner of the net, the village where the fish were caught, and those who helped harvest the catch.

### Contemporary Fishing Methods

Many of the currently used methods are very efficient because the technology and materials used are readily available at a minimal cost. Contemporary methods include hook and line, net fishing (cast, gill, drag, and surround net), spear fishing (snorkel and scuba), hook and gaff, and "other" methods (a miscellaneous category that includes mostly gleaning for invertebrates). These methods, modified through time, are described below and account for the harvest of over 100 species of finfish and 40 nonfinfish species (3 lobster, 9 crab, 24 mollusk, and 4 echinoderm)[2] (Amesbury et al., 1986, 1991).

Currently, the most popular fishing method on Guam is hook and line. This technique ranges from the use of handlines to rod and reel with lures or baited hooks. Recently, we have observed fly fishing in Guam's waters.

The majority of the fish harvested are taken by net fishing. All types of net fishing done today, except gill netting, have long histories on Guam. Net mesh sizes range from 1/4-inch stretch (for seasonal juveniles) to greater than 3-inch stretch. The cast net or throw net (talaya) is one of the few nets that are still hand woven (using monofilament) by the traditional talaya fishermen[3]. These nets vary in mesh size and number of pockets depending on the fish targeted.

Other than the modern equipment, drag netting has changed very little through time. It still is the simplest form of net fishing where the net is pulled through the water as the fish are driven into the net. Today, this method is most often, but not always, used at night.

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[2] This identifies all information, unless otherwise cited, obtained by the authors from Guam Fisheries Investigations-Project FW-2R-26 Job Progress Reports (Jobs: F-F1–2 Inshore Fisheries Survey; F-F1–3 Fisheries Data Processing; F-F1–8 Studies of Recreationally Important Reef Fish). Information can be obtained from the Division of Aquatic & Wildlife Resources (DAWR), Dept. of Agriculture, P.O. Box 2950, Agana, Guam 96910.

[3] D. Narcissi, Talaya fisherman, Guam Environmental Protection Agency, Harmon, Guam 96912. Personal commun.

The use of the surround net or chenchulu has occurred for many years. Today, two types of surround netting occurs. In the first type, two people transport the net through the water on two large inner tubes. The fishermen begin setting the net in a 'U' shape and close the net into a circle as a second group of people drive the fish into the net. Once the net is set, the fishermen dive into the enclosure and harvest the fish by spear and/or hand. The second form of the surround net, also called the atulai gill net (Amesbury et al., 1986), is one that is used to harvest seasonal mackerel or atulai. This net is most commonly used in the harbors, channels, or bays. When a school of atulai is sighted, a boat surrounds the fish with the net and the school can be harvested over a period of days.

Gill net fishing is the most recent form of net fishing on Guam. This method is very popular (usually ranking in the top three of all methods used). This popularity is due to the availability of the gill nets, the comparative low cost, and the effectiveness of the modern monofilament materials. The net is used at any time of the day or night, but it is most successful on an ebb tide where fish escaping the shallows are gilled in the net.

Spearfishing has undergone a vast change with the advent of modern equipment, evolving from handmade spears and freediving to spearfishing with scuba gear. Spearfishing with snorkel and spearfishing with scuba target different fishes and are considered separate techniques. Because of the highly selective nature of both of these methods, spearfishing harvest consists of fish of larger species (i.e., humphead parrotfish, *Bolbometopon muricatum*) than other fishing techniques.

The remaining two methods are primarily used for harvesting nonfinfish. The use of hooks and gaffs targets octopus, although some mantis shrimp and miscellaneous fish are also caught. The last method, a catch-all category appropriately called "other," generally includes gleaning for nonfinfish. New or little-used techniques like dip netting and mantis shrimp traps fall into this miscellaneous category.

## Inshore Creel Survey

The primary objective of the inshore fisheries survey was to obtain the most accurate estimate of the total annual inshore fisheries harvest in order to monitor and manage the resource. Fishing activity has been monitored since the early 1960's when much of the early information was taken by DAWR conservation officers (law enforcement personnel). Monitoring changed over the years, as did fish identification. The early 1960's catch was identified by the Chamoru name of the fish. Problems with catch composition arose because one name could mean any wrasse species, parrotfish would be identified by color (blue, brown, white, and green), and rabbitfish would be identified by at least five names that described the fish by size. As taxonomic skill increased, the catch was reported in increasing detail.

Working closely with the U.S. National Marine Fisheries Service, the DAWR developed a program for analyzing the inshore fisheries. Since the installation, all the data collected has been analyzed by this program. In 1991, we modified and restructured our analysis to allow comparison of data from 1982 to the present. (Because of methodological changes, data prior to 1982 do not lend themselves to analyses.)

### Survey Methodology

Because much of the shoreline is inaccessible to most fishermen (i.e., military bases, clifflines), not all of Guam is surveyed. Data collection for the inshore fisheries expansion is conducted in an area representing 85% of the total fishing participation (verified from shoreline usage seen during aerial surveys). A two-part roving creel survey, effort (or participation) and catch, is performed for both day and night (begun in 1985) to provide sufficient data to allow for 90% confidence limits for the inshore analysis. Detailed methodology and analyses are described in Amesbury et al. (1991).

During an effort survey, a surveyor records all active fishing participation (time of day, location, number of people, number of gear units, fishing methods, reef zone fished, weather conditions, and surf conditions). Counts are made of fishermen and gear and are used to estimate effort in terms of person-hours (p-hr) and gear-hours (g-hr). The catch survey is of the roving fisherman-intercept type and requires as many interviews for as many fishing methods as possible. The survey variables collected include fishing method, number of fishermen, bait type, number of gear, mesh size, interview time, trip length, species caught, numbers of catch species, and individual weights and lengths. Catch data is used to estimate overall landings (kg), CPUE, and species composition.

The majority of the species caught are represented with this methodology. Species that recruit en masse, like mañahak (rabbitfish) or atulai, cannot be adequately represented in the current creel survey. Catch estimates of these species are obtained when the recruiting runs occur and are added to the survey expansion catch values to obtain the yearly inshore harvest.

### Finfish

Finfish are the primary harvest (usually >95%) of contemporary fishing methods. This harvest includes all sizes of reef fish, even the highly anticipated seasonal runs of juveniles. Deepwater and/or pelagic fish, normally harvested using offshore techniques, are occasionally caught using inshore methods. Over 100 species of finfish are harvested in the inshore fishery. The primary families include: Acanthuridae, Carangidae, Gerreidae, Holocentridae, Kyphosidae, Labridae, Lethrinidae, Lutjanidae, Mugilidae, Mullidae, Scaridae, and Siganidae. The top ten species caught in the inshore fishery, not including seasonal juveniles, are *Naso unicornis, Caranx melampygus, Siganus spinus, Mulloides flavolineatus, Lethrinus harak, Valamugil engeli, Kyphosus cinerascens, K. vaigiensis, Cheilinus fasciatus,* and *Gerres* sp. Ranking of these species changes as fishing pressure and gear use fluctuates.

The harvest of one of these key species, *Mulloides flavolineatus*, best describes what is occuring in the finfish fisheries. By 1991, the harvest declined by 90% over a 6-year period (from 33,896 to 3,417 kg). The 100–150 mm size class is targeted in the traditional fishery, which prevents many fish from reaching larger size classes and further impacts the reproductive potential of the population. The downward trend in overall harvest is characterized by the absence of larger females that represent the major portion of the spawning potential.

Many of the once economically important larger species, like the humphead parrotfish, *Bolbometopon muricatum*; wrasse, *Cheilinus undulatus*; groupers over 25 kg, and snappers are rarely seen in Guam's waters, much less reported on the inshore survey catch reports. Interest in the harvest of aquarium fish is on the rise, while the actual harvest appears to be declining. These fish may be less susceptible to overfishing because of their high turnover rate, but problems are beginning to surface with respect to the use of chemicals for fish collecting, habitat destruction, and unmonitored or illegal catches.

The harvest of recruiting juvenile fishes (Table 1) makes up Guam's traditional finfish fishery. It historically has been and still remains an important part of the nearshore reef fisheries. Seasonal juvenile harvest can range from a minor component of <1% (in 1982–83) to over 50% of the overall harvest (in 1991).

Two major components of the juvenile harvest are mañahak and atulai (Fig. 2). The local residents anxiously await the recruitment of both species to the nearshore reef waters. Even though the yearly run of mañahak does not always occur, fishermen will gather at the shoreline during the first few days of the last quarter lunar phase of the expected recruitment period. The mañahak recruit onto the flat area of the reef in aggregations or "balls", as they undergo morphological development from planktivorous to herbivorous fish (Kami and Ikehara, 1976). The largest, as well as the most economically valuable, catch of mañahak is prior to the complete coloration and dietary change (the first 1–2 days on the reef). Harvesting of mañahak is conducted with all nets using a $^1/_4$–$^1/_2$ inch stretch mesh size. Atulai usually begin their seasonal runs into inshore waters by the age of 4 months (Amesbury et al., 1986). The atulai are harvested with surround nets, cast nets, and by hook and line and usually represent the majority of the seasonal harvest.

The recruitment of other juveniles, like i'e' (jacks), ti'ao (goatfish), en masse and aguas (mullet), do not occur like the mañahak or atulai, but they are still heavily fished. The recruitment periods for these juvenile fishes often overlap and peak harvests are seen every 3–4 years. The harvest of these juveniles is primarily by net fishing

**Table 1.—Seasonal juvenile fishes targeted in Guam's traditional finfish fishery. Chamoru names are after Kerr (1990).**

| (English Name)<br>Chamoru name | Family and species targeted |
|---|---|
| Aguas (mullet) | Mugilidae |
| Atulai (bigeye scad, mackerel) | Carangidae; *Selar crumenopthalmus* |
| Achemsom[1] (fusilier) | Caesionidae |
| I'e' (jacks) | Carangidae; primarily *Caranx melampygus* |
| Mañahak (rabbitfish) | Siganidae; *Siganus spinus*, *S. argenteus* |
| Ti'ao (goatfish) | Mullidae; *Mulloides flavolineatus* |

[1] Many local fishermen use this name to incorrectly identify juvenile fusiliers when they recruit en masse. Achemsom actually means small rainbow runner (Carangidae; primarily *Elegatis bipinnulatus*).

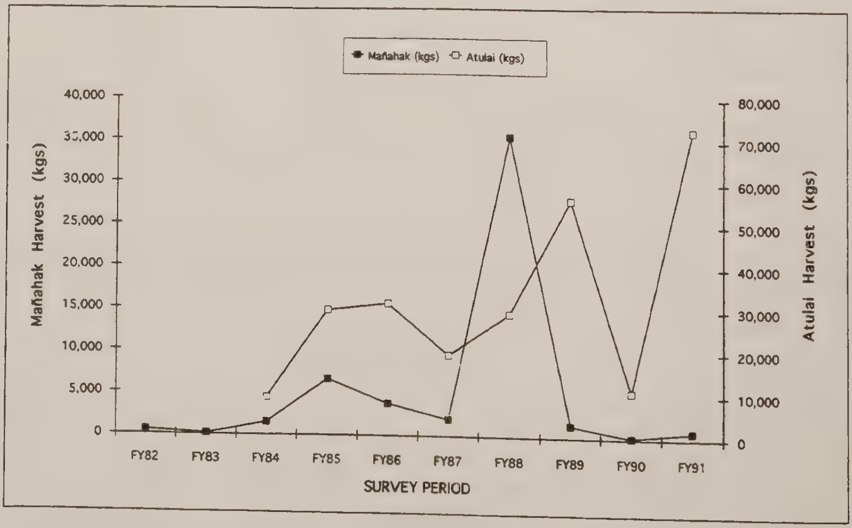

Figure 2.—Estimated harvest from 1982 through 1991 of two of Guam's seasonal juveniles (mañahak = young rabbitfish, primarily *Siganus spinus*; atulai = young mackerel, *Selar crumenopthalmus;* FY = 12-month fiscal year). Names are after Kerr (1990).

(using 1/4–1/2 inch stretch mesh size), except the i'e' which are often harvested by hook and line.

### Nonfinfish

Until recently, the funding constrained the DAWR to work on finfishes only; therefore, information on nonfinfish is limited to catch statistics for methods that also target finfish. Since harvesting of invertebrates is one of the less frequent and easily missed activities (i.e., virtually all lobsters are taken by spearfishing), our nonfinfish harvest is probably underestimated. For a few of the species most often collected, the true annual catch is probably only a few metric tons at most.

The coral reef is Guam's single most valuable resource, and, over the years, coral has been harvested for ornamental and commercial use. The most common corals harvested commercially in the past included *Acropora*, *Antipathes*, *Fungia*, *Heliopora,* and *Tubipora* sp. (Hedlund, 1977). Coral (dead or live) is no longer legally collected without a permit (now issued for educational or research purposes only), and the regulation is strictly enforced.

Two species of green algae (*Caulerpa racemosa* and *Codium* sp.), two species of red algae (*Gracilaria edulis* and *Asperagopsis* sp.) and one species of brown algae (*Sargassum polycystum*) are commonly harvested (Hedlund, 1977). The green algae or seaweed is seasonal (usually January through May) and when collected, is often sold at local markets. Sargassum and *Enteromorpha* sp. are also collected as bait for rod and reel fishing for herbivores[4].

Many molluscan species have been and are still harvested on Guam. About 15 bivalve species (3 of which are tridacnid clams) have been harvested on Guam (Stojkovich and Smith, 1978). Other shelled mollusks collected include *Trochus* sp. (topshell or aliling), chitons, conchs, nerites, and strombids (Smith, 1986). A few of these mollusks (plus some not mentioned) are collected for ornamental use. The octopus is the most sought after unshelled mollusk; squid and cuttlefish form part of the incidental catch. Of all these, only *Trochus* has a fisheries potential and is currently regulated with size restrictions and is strictly monitored.

Crustaceans make up a major portion of the nonfinfish catch. About nine species of crab are hunted, including land and marine crabs. *Carpilus maculatus* (7–11 crab) and *Etisus splendens* are primarily targeted, whereas *Calappa hepatica* and rarely *C. calappa* (box crabs) are taken as incidental catch during net fishing, spearfishing, or gleaning. Two species of land crabs (*Cardisoma carnifex* and *Birgus latro*) are also highly prized, but are not monitored on the inshore fisheries surveys. Lobster catches are highly prized. The following species are identified in Guam's catches: Palinuridae (*Panulirus longipes*, *P. ornatus*, *P. pencillatus*, *P. versicolor*), Homaridae, and Scyllaridae. The spiny lobster, primarily *P. pencillatus* and the slipper lobster, *Scyllarides squamosus*, are the two main components of the inshore lobster catch and are harvested by spearfishing and "other" techniques (i.e., gleaning). Mantis shrimp, another crustacean, is often mistaken for lobster by some fishermen. It is harvested by hooks and gaffs, shrimp traps, and through incidental catches.

Smith (1986) stated that other invertebrates harvested have included two species of sea urchins (*Tripneustes gratilla* and *Echinometra mathaei*), two species of sea cucumbers (*Stichopus horrens* and *Holothuria atra*) and a freshwater shrimp (*Macrobrachium* sp.). The sea urchin *T. gratilla* has been harvested for ripe gonads. The harvest of sea cucumbers is sporadic (*H. atra* is the most common species harvested). Present harvest is less than that reported in the late 1800's, when catches of 2–3 tons were documented (Amesbury et al., 1986).

Five species of sea turtles have been identified in Guam's waters[5]. Harvest of sea turtles on Guam was prominent prior to World War II and occurred legally until 1976. Inshore catch reports for 1967–68 noted landings of over 80 turtles in 18 months, the largest individuals weighing an estimated 450 pounds. It is currently difficult to determine the extent of the actual catch because of the illegal nature of this activity. Examples of significant poaching activities were seen during a 2-week period in 1990–91, when an estimated 20 turtles (in two separate incidents) were poached.

### Catch and Effort Estimates

Overall catch values for 1982–91 for all fish caught (finfish, nonfinfish, and seasonals) for both day and night are shown in Figure 3. In 1990, the participation declined to less than 50% (42,294 fishermen) of the 1984 high (107,391 fishermen). Similar trends for effort and catch are seen (Fig. 3) where the highs occurred in 1984, but lows occurred in 1989 and 1990. Effort and participation increased in 1991 and are attributed to an excellent year for seasonal juvenile harvest. If harvest estimates for atulai and mañahak (Fig. 2) were removed from the catch values, the overall harvest falls between 1989 and 1990 estimates. The 3–4 year pulse of other juveniles (i'e', aguas, and ti'ao) was also observed in 1991 and falsely elevated the survey estimates (number of participants, gear, catch, etc.). If the juvenile harvest values were removed from all years, the 1991 harvest estimate would still be smaller than any previous year.

### Day Fishing Estimates

Day harvest and effort values for means for reef fisheries during 1982–91 are shown in Figure 4. A 60% decline in the number of fishermen occurred in 1990 (30,396) from a high in 1984 (97,603). Similar trends for inshore finfish are seen for both effort and catch (Fig. 4) where highs occurred in 1984. Catch follows effort until 1988 when harvest continues to drop while the effort increases. Nonfinfish effort declined over 90% by 1989 (2,759g-hr) from a high in 1982 (28,613 g-hr). Harvest of nonfinfish, though underestimated, declined from 29,499 kg in 1982 to 1,289 kg in 1990. Both finfish and nonfinfish show declines in effort and harvest estimates for 1988–91 as compared with the 1982-87 period.

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[4] R. A. Hensley, DAWR, P.O. Box 2950, Agana, Guam 96910. Personal observ.

[5] Hensley, R. A. The distribution and abundance of marine turtles from 1966 to 1992 in the waters of Guam. Texas Parks and Wildlife Department, 1231 Agnes St., Corpus Christi, TX 78401. Unpubl. manuscr.

## Night Fishing Estimates

During the night surveys from 1985 through 1991, effort reached a high for finfish in 1987 (58,893 g-hr) and declined more than 50% to a low in 1990 (25,181 g-hr). Night harvest of finfish rose to a high of 23,538 kg in 1988 before declining to less than 50% in 1991 (10,285 kg). Nonfinfish showed little change in effort until the drop in 1989–90 (from >2,000 to 340 g-hr). The overall night harvest was composed of nonfinfish harvest that ranged from 3.2% (361 kg) in 1989 to 23% (4,684 kg) in 1986.

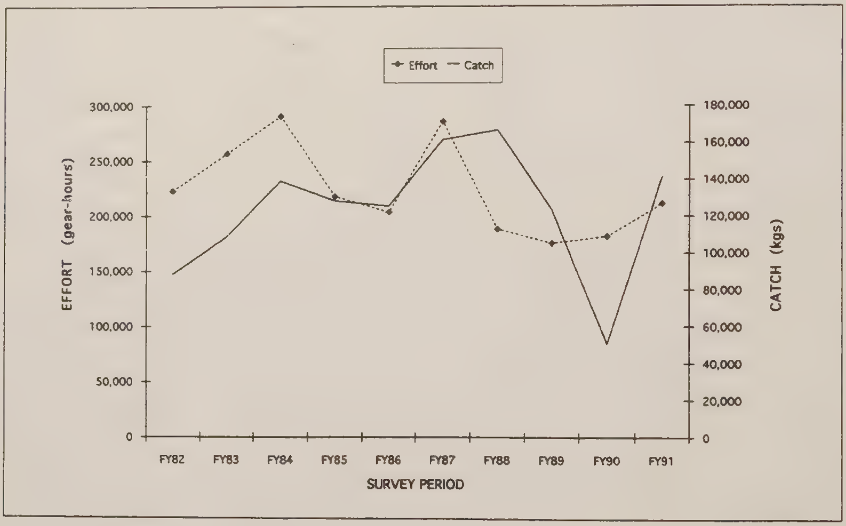

Figure 3.—Estimated effort and harvest of Guam's nearshore reef fisheries from 1982 through 1991 (catch = harvest of all finfish and nonfinfish for both day and night, FY = 12-month fiscal year).

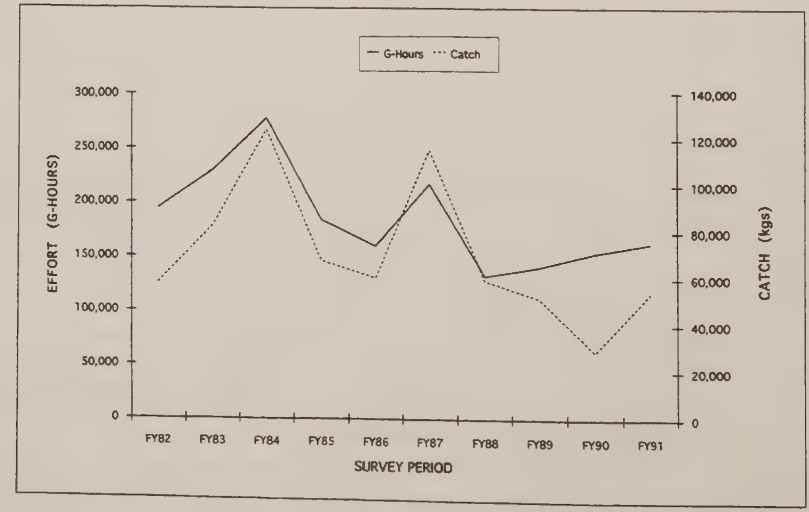

Figure 4.—Estimated effort catch of Guam's inshore fisheries for the daytime from 1982 through 1991 (catch = total harvest of finfish without mañahak or atulai harvest, FY = 12-month fiscal year).

## Gear Usage and CPUE

The most popular fishing methods for day and night are seen in Figures 5 and 6, respectively. Hook and line is the most popular method for both day and night, but consistently has one of the lowest CPUE's (catch per unit of effort) ranging from 0.05 to 0.36 for both day and night. The second and third most popular methods for day fishing are cast and gill net. During 1982–84, "other" displaced gill net from the top three. After 1985, most of the participation can be seen with the top three methods (hook and line, cast net, and gill net).

Figure 6 shows the most popular night fishing methods. Spearfishing with snorkel gear ranks second, more often than gill net, drag net, or "other"methods. Except in 1985, when "other" displaces gill net from its third ranking, gill net fishing has increased in popularity where it ranked second for 1986–91.

Many gear use fluctuations are due to the popularity of methods with high CPUE's. The highest day CPUE's (usually about 2.0–4.7) are most often seen with net fishing (mainly drag net, surround net, and gill net) followed by slightly lower CPUE's for spearfishing with scuba and "other". Night CPUE's fluctuate more than day CPUE's and are highest for spearfishing, drag netting, and gill netting. Much of the CPUE fluctuations, especially with net fishing methods like cast, drag, and gill net, can be attributed to the seasonal aspect of the fisheries with respect to traditional fish harvests.

## Research

The DAWR has been involved in many aspects of research. For many years, aquaculture potential for freshwater finfish was investigated. Currently, aquaculture research is still conducted (marine finfish and invertebrates) and involves another government agency, private companies, and the University of Guam. Most recently, DAWR began a study of the feasibility of restocking the giant clam *Tridacna derasa*. Studies on the biology and life histories of some recreationally important fishes began in 1984. To date, *Siganus spinus* and *Mulloides flavolineatus* biological profiles have been completed, with *Lethrinus harak* in progress. These biological investigations have been aided by the graduate program at the University of Guam where students investigate important species like *Acanthurus triostegus*, *A. lineatus*, and *Naso literatus* (Molina, 1983; Davis, 1985). Even with the research being done by local and visiting scientists, there is still an enormous amount of information lacking on Guam's fishes.

Work toward identifying the many fish species in Guam's waters has occurred (Kami et al., 1968; Kami, 1971, 1975; Myers and Shepard, 1980; Shepard and Myers, 1981; Amesbury and Myers, 1982; Myers, 1988, 1989). This documentation continues as new species are recorded. The species composition of the fishery on Guam has been made possible by the various check-lists of the fishes in Guam's waters. Aerial surveys are periodically performed to monitor inshore fishing activity in nonsurveyed areas of Guam. Incidental information acquired includes offshore fishing information and turtle abundances[5].

Future investigations are planned for other recreationally important reef species to make sound management suggestions (size, bag limits, seasonal closures). Otolith work has been initiated through the University of Guam.

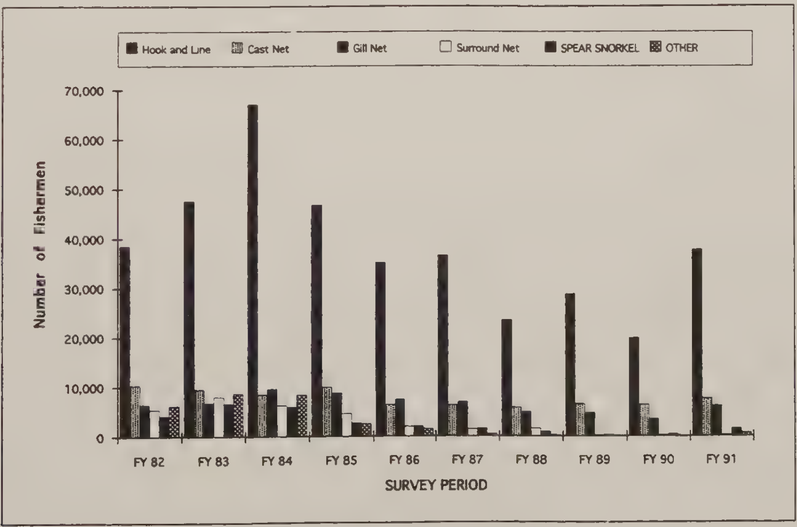

Figure 5.—The most popular fishing methods in Guam's inshore fisheries for the day from 1982 through 1991 (number of fishermen = number of people using specific method; FY = 12-month fiscal year.)

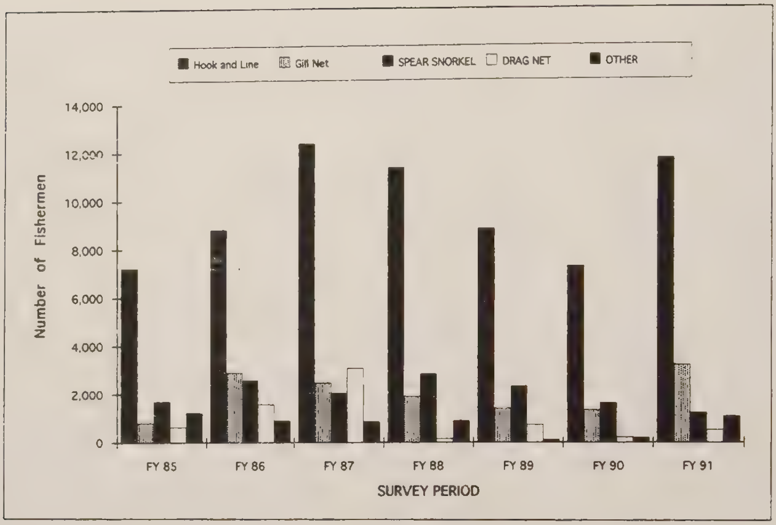

Figure 6.—The most popular fishing methods in Guam's inshore fisheries for the night from 1985 through 1991 (number of fishermen = number of people using specific method, FY = 12-month year).

Analyses of the stocks and future fishing potential is continuing through the modifications in existing expansion methodology and creel survey information[6].

### Management Concerns

As the human population grows, modern fishing techniques improve, and fish stocks decline, the need for the management of Guam's tropical coral-reef fisheries increases in order to protect the reef habitat from overfishing as well as from pollution and destruction. The effects of pollution are seen as a result of development and population growth. Much of Guam's southwestern coral reefs are covered with silt from freshwater runoff. Because water quality is extremely important to viable coral reefs (and fish populations), strict standards for development, land clearing, and chemical use should be initiated and enforced. Other major causes of reef destruction includes the use of explosives and poisoning (chlorine bleach and *Barringtonia* root) as fishing methods. Both types of fishing are illegal, but through an education program (with respect to problems associated with destructive fishing practices) and strict enforcement, these have been declining.

Besides pollution and destruction of the reef habitat, it is imperative that a comprehensive management program be established for Guam's fisheries. There are enough indicators that fishing pressure on Guam's inshore resources has reached the point of overexploitation of many of the key species. The proportion of juvenile fish in fisheries landings is increasing rapidly. "Growth overharvesting" has been occurring, and the overall yield has declined as a larger and larger portion of smaller fish are harvested. It is very likely that "recruitment overharvesting," where the reproduction and recruitment of the stocks show a decline, is currently occuring in some of the recreationally important species.

### Management Recommendations

Currently, there are several seasonal, area, gear, and size restrictions and bag limits on Guamanian fisheries. These pertain mostly to nonfinfish such as the spiny lobsters, tridacnid clams, *Trochus,* and crabs. Gear restrictions are the only regulations pertaining to finfish harvest. Minimum mesh sizes of 1 1/2 inches on gill nets (except for traditional or juvenile harvest) and hook restrictions for atulai (no snagging) are the principal restrictions. Other gear restrictions include length and time limits for gill net fishing and the prohibited use of fish weirs.

New regulations are currently awaiting approval with one of the most promising avenues being the development of marine conservation area(s). These should be established to provide a refuge for recreationally important fish so they can grow, mature, and reproduce to increase stock health and recruitment. Besides the ability of an area closure to protect fish from harvest, there are many other benefits that make this an increasingly popular form of management and conservation. The closure limits the catches on adjacent reefs without closing down the entire fishery and provides areas where user conflicts are minimized.

Gear restrictions should be implemented and enforced. Because no other method for the seasonal harvest (with mesh sizes as small as 1/4 inch) is as dangerous to the entire fishery as the nonselective method of gillnet fishing, this method should be heavily regulated. The minimum mesh size for gill nets should be 3 inches, maximum length of time used should be decreased, and it should be required that all nets be manned at all times. The use of gill nets for juvenile fish harvest should be eliminated (except atulai where a $1^{1}/_{2}$-inch minimum mesh size should be kept). Other nets, like cast nets and drag nets could still be used for juvenile harvest without the damage to the fish stocks that gill netting may cause. All commercial fishing for seasonal juveniles using nets with mesh sizes less than $1^{1}/_{2}$ inches should be prohibited. Because of the environmental damage that sometimes occurs with drag nets, the use of this method should be restricted to specific areas where minimal destruction of habitat would occur. Spearfishing with scuba gear should be prohibited because the few remaining large fish of overexploited species are being targeted.

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[6] Hensley, R. A., and T. S. Sherwood. Unpubl. data. Texas Parks and Wildlife Department, 1231 Agnes St., Corpus Christi, TX 78401.

Appropriate management strategies are difficult to develop when dealing with multispecies, multigear fisheries. Management is further impeded by the desire to hold on to traditional fishing activities which involve the harvest of juvenile fishes. To ensure that future generations enjoy the traditional harvest of juveniles as well as other fishes, strict management regulations must be implemented. Of course, the ability of any management approach also depends on ensuring a healthy and clean reef environment to provide adequate habitat and optimal reproduction.

## Market Description

The DAWR has been keeping track of the catch sold by offshore recreational fishermen (Myers, 1993) and has recently begun to document other catches, including nearshore reef fishes. The market for nearshore reef fish has increased on Guam, especially with the diverse cultures that eat fish as a primary source of protein. With the influx of new people and the desire for local fresh fish, the market continues to expand. Because the prices are high, with the average price of \$3–4/pound for whole reef fish, the financial benefit for fishermen using a high CPUE method (gill net, surround net, drag net) is enormous. Many of the net fishermen encountered on the inshore survey are no longer subsistence fishermen but are commercial fishermen.

Reef fish imports from Belau and the Federated States of Micronesia are increasing. It is difficult to determine the amount of fish imported because few restrictions are placed on importation. Further difficulties occur in monitoring sales of local and imported fish because of the manner in which they are sold. Many fishermen sell their catch on the roadside, while others sell to small local stores or the large supermarkets. Continued monitoring is necessary to obtain more knowledge of the commercial aspect of the inshore fisheries.

## The Future

The outlook for Guam's inshore fisheries, given the current catch information, is poor. If management strategies are not incorporated soon, the remaining fishery may continue to decline to the point of poor productivity. The need for fishery imports will continue to increase as local stocks decline. This lower abundance and availability of Guam's fishery resources could cause higher fishing pressure on neighboring islands.

The ability to manage Guam's fisheries is limited by local politics. In an effort to protect the traditional fishing practices of the Chamorus, legislation has been passed without any apparent foresight of impact on other aspects of the fishery. Interpretation of the term "traditional" has allowed fishing practices acquired since WWII (i.e., gill netting) to continue with little to no regulation. If allowed to continue, the change from subsistence fishing to "traditional" commercial fishing will continue to strain Guam's fishery resources.

The picture is not as bleak as it may appear, however, because many Guamanians are beginning to become environmentally aware. This is demonstrated by the increasingly high number of informants regarding illegal fishing practices (turtle poaching, coral harvesting, gill net abandonment, etc.). The DAWR continues to address the aspect of educating tourists (over 740,000 in 1990) and temporary workers from foreign lands about local regulations. As Guam's population and a need for housing increases, illustrated by the recent closure of the U.S. military bases in the Philippines and the subsequent transfer of 2,000 families to Guam, we see greater threats to the reef resources than we have now. With the help of the general population and the passage of rigid regulations, there is still hope for the fishery to rebound. However, it is highly unlikely for future harvests to reach pre-1987 totals.

## Acknowledgments

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# Dispersion and abundance of Antarctic krill in the vicinity of Elephant Island in the 1992 austral summer

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ABSTRACT: Antarctic krill *Euphausia superba* distribution and abundance were estimated from 4 acoustic surveys conducted in the vicinity of Elephant Island, Antarctica, from mid-January to mid-March 1992. The first and last surveys covered a 105 by 105 n mile study area centered on Elephant Island; the second and third surveys covered a 60 by 35 n mile area immediately north of Elephant Island. During the first survey, krill were distributed in a wide band extending along the north side of Elephant Island and wrapping around the western end; biomass was estimated to be 2.2 million metric tons (t). During the second survey, the highest densities of krill were over the shelf extending to the northwest from Elephant Island and including the Seal Island archipelago; high densities of krill also extended off the shelf from the northeast end of Elephant Island into deeper water. Biomass in the smaller survey area was estimated to be 0.7 million t. Three weeks later, high krill densities were still apparent in the vicinity of Seal Island, but the area of high density previously mapped off the northeast end of Elephant Island had diminished considerably; biomass was estimated to be 0.4 million t. During the final survey, conducted 6 wk after the first survey, krill were mapped in reduced densities primarily to the west of Elephant Island; biomass over the larger survey area had declined to 1.1 million t.

## INTRODUCTION

Antarctic krill *Euphausia superba* is a key component in the pelagic marine ecosystem of the Southern Ocean (Laws 1985). As much as 300 million metric tons (t) of krill may be consumed annually by 30 million pinnipeds, 50 million sea birds and 300 000 baleen whales (Miller & Hampton 1989). It is also the target of an international fishery (ca 400 000 t annually). Although the harvest is less than 1% of the annual krill production, catches tend to be localized near penguin and fur seal breeding colonies (Agnew in press). The effects of fishing, however, on the reproductive success of land-breeding krill predators has yet to be demonstrated. To do so, it will first be necessary to document the response of predator populations to features of the offshore prey field, and then to determine the effects of fishing on the distribution of prey.

In response to international concern regarding unregulated development of fisheries in the Southern Ocean, the Convention of the Conservation of Antarctic Marine Living Resources (CCAMLR) was established as part of the Antarctic treaty system in 1982. A principal tenet of the convention is that the harvest of living resources shall be managed with the goal of preserving species diversity and stability of the entire marine ecosystem. Through its Scientific Committee, CCAMLR has encouraged member nations to establish long-term programs to monitor foraging behavior and reproductive success of selected krill predators (SC-CAMLR-IV 1985, SC-CAMLR-V 1986, Croxall et al. 1988, Croxall 1989). More recently the Scientific Committee called for descriptions of the prey distribution and abundance in the vicinity of predator monitoring sites and adopted a series of general principles to be used in the design of krill surveys (SC-CAMLR-X 1991). It was recommended that: (1) acoustic data be collected along a series of regularly spaced parallel transects; (2) these data be used to map the distribution

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of krill in the vicinity of a predator monitoring site and estimate their abundance; and (3) more focused surveys, consisting of randomly or regularly spaced parallel transects, be conducted in areas of highest krill density.

A seasonal predator monitoring site has been maintained at Seal Island, off the northwest coast of Elephant Island, Antarctica, since the austral summer of 1986/1987 (Bengtson et al. 1991, Boveng et al. 1991, Croll et al. 1991). An annual series of complementary shipboard observations, including acoustic surveys of zooplankton distribution and abundance, has been conducted in the waters surrounding Elephant Island (Anon. 1990, Rosenberg & Hewitt 1991, 1992). The acoustic surveys presented in this report are the latest in the series.

Results from previous surveys suggest that the distribution, abundance and demography of krill in the Elephant Island area varies considerably both within and between years (Mathisen & Macaulay 1983, Kalinowski 1984, Macaulay et al. 1984, Kalinowski et al. 1985, Klindt 1986, Nast 1986, Siegel 1986b, Brinton et al. 1987), and that these changes are due to immigration and emigration of krill rather than local population effects (Priddle 1988, Sahrhage et al. 1988). Spatial separation of adults, sub-adults and juveniles suggests that offshore waters west of the Antarctic Peninsula are krill spawning areas and that the neritic zone may be used as nursery grounds (Fevolden & George 1984, Quetin & Ross 1984, Siegel 1986a). Siegel (1988) proposed that adult krill migrate from the southwest (Bellingshausen Sea) into offshore waters during the summer, that sub-adults and juveniles drift to the northeast with the prevailing coastal current, and that the direction of these movements is reversed the autumn. Makaorov et al. (1988) and Nast et al. (1988) noted that Elephant Island lies in the path of a major outlet from the Weddell Sea, and that variations in the position of the Weddell-Scotia Confluence (WSC) may account for the variation in the numbers of krill accumulating in the Elephant Island area from the northern Weddell Sea. Stein (1986) described seasonal variations and meanders in the position of the WSC, which is apparent as a persistent hydrographic front north of Elephant Island. The meanders and eddies in the current flow along the front may be a factor favoring the accumulation of krill in the Elephant Island area, regardless of their origin (Everson 1984, Witek et al. 1988).

Two objectives of our field research program are to: (1) relate the response of krill predators to changes in the availability of their prey; and (2) relate these changes to biotic and abiotic aspects of the pelagic habitat. As such, there is interest in both the spatial patterns of krill distribution as well as their abundance. The analyses presented here were conducted to reveal features of krill distribution that persisted over relatively large scales (tens of km, and several days). Analyses of these data on finer scales will be reported elsewhere.

## METHODS

Echo integration methods were used to map the distribution of krill and estimate its abundance in the vicinity of Elephant Island. Four surveys were conducted between 19 January and 11 March 1992 (Fig. 1a, b).

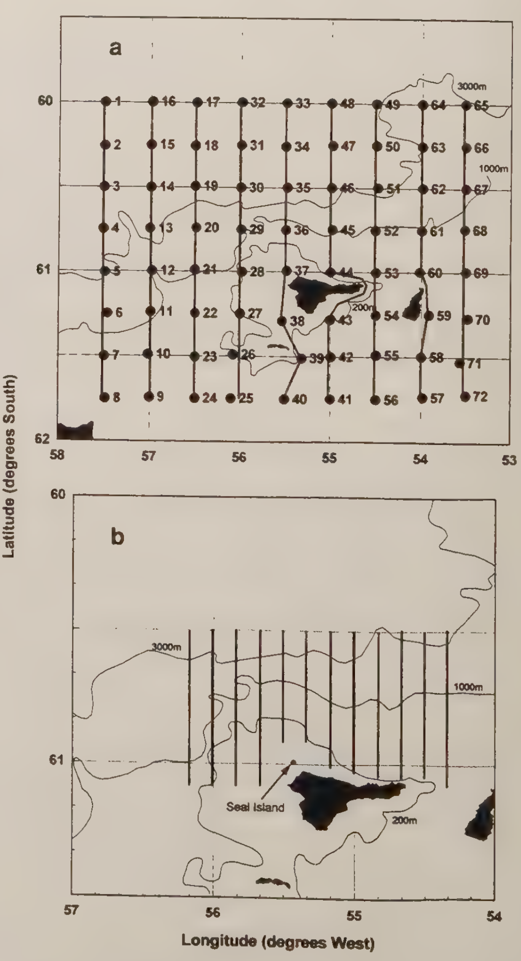

Fig. 1. (a) Station pattern and acoustic transects for Surveys A and D. (b) Acoustic transects for Surveys B and C

Surveys A and D were designed to describe meso-scale (tens to hundreds of km) features of water mass structure, phytoplankton biomass and productivity, and zooplankton constituents (including krill) in the area around Elephant Island. Surveys B and C were designed to map the micro-scale (one to tens of km) features of the distribution, density and abundance of krill immediately north of Elephant Island, within the foraging range of krill predators breeding at Seal Island.

Acoustic data were collected with a Simrad EK500 echo sounder (Bodholt et al. 1989) configured with a 120 kHz split-beam transducer. The transducer was deployed on a dead-weight towed body positioned 7 m below the water surface, and communicated with the echo sounder via 50 m of armored towing cable, a set of slip rings on the towing winch, and 75 m of shielded deck cable. The entire system (echo sounder, cables and winch) was calibrated before and after the cruise using standard sphere methods (Johannesson & Mitson 1983) in a 3 m diameter by 10 m deep tank filled with seawater chilled to 0.5 °C; calibration drift was less than 1.2 dB (Demer & Hewitt in press).

Echo power levels for each ping were sampled approximately every 3 cm (25 kHz sampling rate) and adjustments were made for spherical spreading and absorption losses. This data set was averaged every 0.5 m over depths ranging from 10 to 250 m, and the resulting set of mean volume backscattering strength measurements ($s_V$) was passed to a computer for further processing and archiving.

Echograms were generated from the subsampled data set and interpreted. The threshold volume backscattering strength was set at −81 dB (equivalent to approximately 0.1 krill $m^{-3}$), and portions of the echogram were attributed to echoes from krill and non-krill (bottom return, system noise, other scatterers). For the purpose of generating distribution maps and biomass estimates, volume backscattering strength attributed to krill was integrated over 10 to 250 m depth range (or 1 m above the bottom, if shallower than 250 m) and averaged over 1 n mile intervals. Ship's position was also recorded every 10 s and time-keyed to the acoustic data set. Version 2.6 of the 'Bergen Integrator' software, co-developed by the Bergen Institute of Marine Research, the Christian Michelsen Institute, and Simrad (Knudsen 1990, Foote et al. 1991), was used as an aid in interpreting the echograms and archiving the results.

Mean backscattering area per square n mile of sea surface ($s_A$) for every 1 n mile of survey transect [$m^2$(n mile)$^2$] was thus calculated by the Bergen Integrator software as:

$$s_A = 4\pi r_0^2 1852^2 \int_{z=10}^{z=250} s_V \, dz \qquad (1)$$

where $s_V = 0$ if $10 \log(s_V) \leq -81$ dB; $z$ = depth; and $r_0$ = 1 m is the reference range for backscattering strength.

By assuming that measurements of $s_V$ represent the linear sum of echoes from individual animals within the sample volume (MacLennan & Simmonds 1992), the numerical density of krill (number per unit area of sea surface) can be estimated by dividing $s_A$ by the backscattering cross-sectional area ($\sigma$, $m^2$) of a single krill. Biomass density of krill ($\rho$, g $m^{-2}$) can be estimated by multiplying the numerical density by the weight of a single krill.

Both the backscattering cross-sectional area and the weight of krill are non-linear functions of body length. We used the definition of krill target strength (*TS*, dB) as a function of standard length ($l$) as proposed by Greene et al. (1991) and adopted by the CCAMLR Working Group on Krill (SC-CAMLR-X 1991) (see also 'Discussion'):

$$TS = -127.45 + 34.85 \log_{10}(l) \qquad (2)$$

where $l$ = standard length of krill (mm). The corresponding backscattering cross-sectional area of krill ($\sigma$) is:

$$\sigma = 4\pi r_0^2 10^{-12.745} l^{3.485} \qquad (3)$$

The relationship of krill wet wt ($w$, mg) as a function of standard length was taken from Siegel (1986a) for individuals caught in March:

$$w = 0.00193\, l^{3.325} \qquad (4)$$

Thus:

$$\rho = s_A \frac{w}{\sigma} = 0.249\, l^{-0.16} s_A \qquad (5)$$

Krill were sampled directly with a 6 ft (ca 1.8 m) Isaacs-Kidd midwater trawl (IKMT, Devereux 1953), outfitted with a net made of 505 µm mesh nytex, and fished obliquely from approximately 170 m depth to the surface (Loeb & Siegel in press). Net tows were made at regularly-spaced stations on Surveys A and D (Fig. 1a) without regard to time of day; no net tows were conducted during Surveys B and C. The frequency distribution of krill standard length was used to calculate $\rho$ as follows:

$$\rho = 0.249 \sum_{i=1}^{n} f_i (l_i)^{-0.16} s_A \qquad (6)$$

where $f_i$ = the relative frequency of krill of standard length $l_i$, such that $\sum_{i=1}^{n} f_i = 1$, where $i$ refers to the $i$th length class and $n$ is the number of length classes.

A composite frequency distribution of krill standard length was calculated from all net tows conducted during Survey A and used to estimate densities on Surveys A and B; similarly a composite frequency distribution was calculated from all net tows conducted during Survey D and used to estimate densities on Surveys C and D. The resulting data sets, indexed by time and ship's position, were gridded and contoured for each of the 4 surveys.

Following the method proposed by Hampton (1987) and Jolly & Hampton (1990), each transect was considered a single sample of biomass density. The entire survey area was treated as a single stratum. Mean biomass density ($\bar{\rho}$) was calculated as a weighted mean:

$$\bar{\rho} = \frac{\sum_{i=1}^{N} \bar{\rho}_i (n_i)}{\sum_{i=1}^{N} n_i} \tag{7}$$

where $\bar{\rho}_i$ = mean density on the *i*th transect; $n_i$ = no. of 1 n mile averaging-intervals on the *i*th transect; and N = no. of transects. Following Jolly & Hampton (1990) and Simmonds et al. (1991), variance of $\bar{\rho}$ was estimated as:

$$\bar{\rho} = \frac{N}{N-1} \frac{\sum_{i=1}^{N} (\bar{\rho}_i - \bar{\rho})^2 n_i^2}{\left(\sum_{i=1}^{N} n_i\right)^2} \tag{8}$$

Biomass was estimated as:

$$B = A(\bar{\rho}) \tag{9}$$

where $A$ = total survey area (m$^2$). Variance of the biomass estimate was calculated as:

$$\text{var}(B) = A^2 \text{var}(\bar{\rho}) \tag{10}$$

and the coefficient of variation as:

$$\text{CV} = \frac{\sqrt{\text{var}(B)}}{B} \tag{11}$$

The above expression only reflects the sampling variance (Simmonds et al. 1991). Other potential sources of errors and biases are outlined in the 'Discussion'.

## RESULTS

In late January, krill were distributed in a broad band which extended across the north side of Elephant Island and wrapped around its western end (Survey A, Fig. 2). During a higher resolution survey, conducted during the first week in February, highest krill densities were mapped over the shelf extending to the northwest from Elephant Island and including the Seal Island archipelago. High densities of krill also extended off the shelf from the northeast end of Elephant Island into deeper water (Survey B, Fig. 3).

A similar survey was conducted 3 wk later during the last week in February. Although high krill densities were still apparent in the vicinity of Seal Island, the area of high density previously mapped off the northeast end of Elephant Island had diminished considerably (Survey C, Fig. 4). A final survey, similar in areal coverage and sampling intensity to the first survey, was conducted during the first 10 d of March, 6 wk after Survey A. Both the extent and density of krill were greatly reduced; areas of highest densities were mapped to the west of Elephant Island (Survey D, Fig. 5).

The frequency distribution of krill standard length was bimodal throughout the study period (Fig. 6). Both

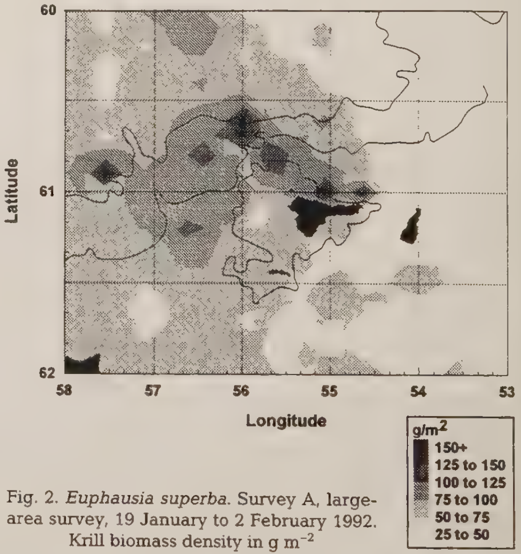

Fig. 2. *Euphausia superba*. Survey A, large-area survey, 19 January to 2 February 1992. Krill biomass density in g m$^{-2}$

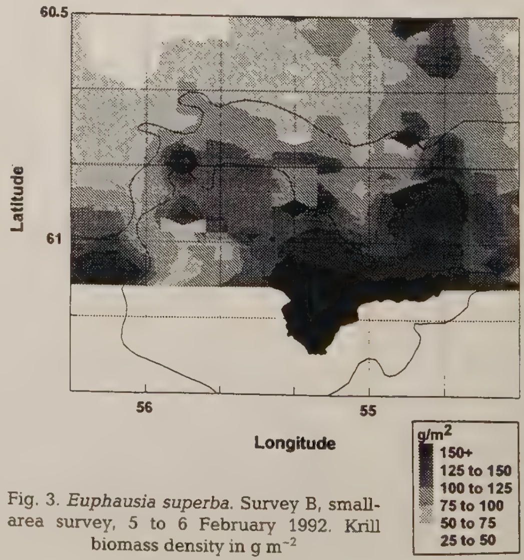

Fig. 3. *Euphausia superba*. Survey B, small-area survey, 5 to 6 February 1992. Krill biomass density in g m$^{-2}$

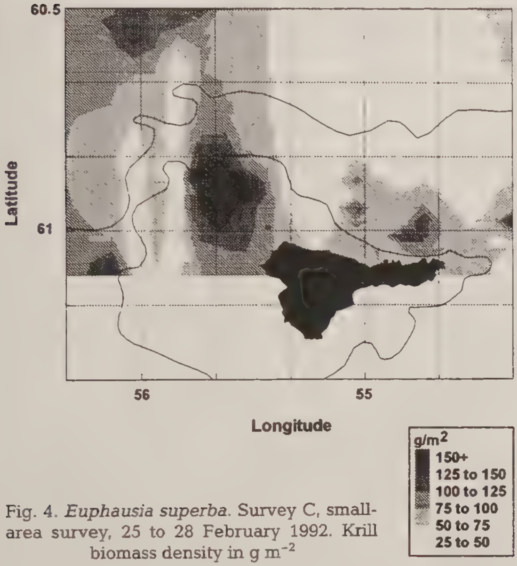

Fig. 4. *Euphausia superba*. Survey C, small-area survey, 25 to 28 February 1992. Krill biomass density in g $m^{-2}$

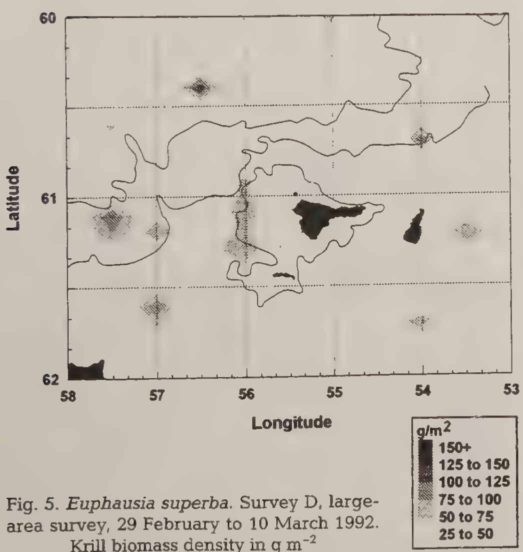

Fig. 5. *Euphausia superba*. Survey D, large-area survey, 29 February to 10 March 1992. Krill biomass density in g $m^{-2}$

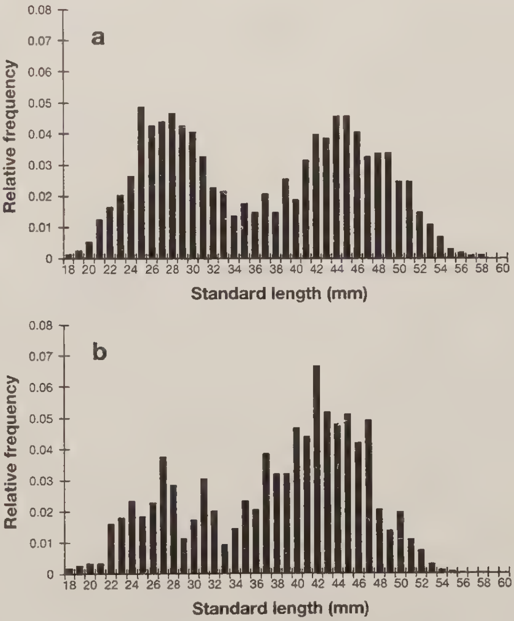

Fig. 6. *Euphausia superba*. Frequency distributions of krill standard length collected during (a) Survey A and (b) Survey B. From Loeb & Siegel (in press)

reproductively mature and immature adult krill contributed to the mode at 44 to 45 mm; juvenile krill constituted the mode at approximately 28 mm (Loeb & Siegel in press). Relative to Survey A, greater proportions of intermediate-sized krill and reduced proportions of smaller sizes were caught during Survey D. The size frequency obtained during Survey A was used to calculate krill densities on Surveys A and B, and the size frequency of krill obtained during Survey D was used to calculate krill densities on Surveys C and D.

During the first large-area survey (Survey A) krill abundance was estimated at 2.2 million t, CV = 16 %. Six weeks later (Survey D) krill abundance over the same area was estimated to be 1.1 million t, CV = 9 %. Estimated abundance during the first small-area survey (Survey B) was 0.7 million t, CV = 22 %, and during the second small-area survey (Survey C) it was 0.4 million t, CV = 23 % (Table 1).

## DISCUSSION

Several sources of error associated with the echo integration method can be identified. These include both random errors and systematic biases associated with the definition of individual krill target strength, estimating the size distribution of krill in the surveyed population, species identification, estimating the amount of undetected krill, assumption of a linear addition of echoes from individual krill in the sample volume, estimating system gain and absorption loss, and estimating survey sampling error.

Table 1. *Euphausia superba*. Abundance estimates for Surveys A, B, C and D. $n_i$: no. of 1 n mile averaging intervals on the *i*th transect; $s_A$: mean backscattering area per n mile$^2$ of sea surface; $\bar{\rho}$: mean biomass density; Var ($\bar{\rho}$): variance of $\bar{\rho}$; CV: coefficient of variation

| | Survey A | | Survey B | | Survey C | | Survey D | |
|---|---|---|---|---|---|---|---|---|
| | $n_i$ | $s_A$ | $n_i$ | $s_A$ | $n_i$ | $s_A$ | $n_i$ | $s_A$ |
| Transect 1 | 113 | 386.3 | 30 | 714.9 | 47 | 725.9 | 110 | 264.0 |
| Transect 2 | 95 | 374.5 | 37 | 188.6 | 35 | 512.7 | 98 | 254.8 |
| Transect 3 | 108 | 814.9 | 35 | 979.5 | 38 | 160.5 | 103 | 223.1 |
| Transect 4 | 112 | 590.6 | 35 | 470.7 | 37 | 1155.2 | 106 | 332.9 |
| Transect 5 | 127 | 451.1 | 27 | 386.9 | 29 | 648.0 | 110 | 150.0 |
| Transect 6 | 137 | 473.4 | 24 | 590.0 | 25 | 55.2 | 133 | 169.9 |
| Transect 7 | 115 | 231.5 | 31 | 918.2 | 29 | 34.9 | 109 | 166.6 |
| Transect 8 | 117 | 178.9 | 28 | 67.8 | 37 | 400.5 | 116 | 192.8 |
| Transect 9 | – | – | 37 | 1220.0 | 32 | 219.9 | 116 | 174.4 |
| Transect 10 | – | – | 35 | 1990.3 | 37 | 337.5 | – | – |
| Transect 11 | – | – | 33 | 353.5 | 32 | 144.6 | – | – |
| Transect 12 | – | – | 34 | 529.6 | 38 | 374.1 | – | – |
| $\sum n_i$ | 924 | | 386 | | 416 | | 1001 | |
| Weighted mean | 436.2 | | 721.8 | | 421.3 | | 211.9 | |
| Weighted variance | 4722.5 | | 25723.2 | | 9056.1 | | 383.9 | |
| $0.249\sum_{i=1}^{n} f_i(l_i)^{-0.16}$ | 0.1403 | | 0.1403 | | 0.1398 | | 0.1398 | |
| $\bar{\rho}$(g m$^{-2}$) | 61.20 | | 101.27 | | 58.90 | | 29.63 | |
| Var ($\bar{\rho}$) | 92.96 | | 506.34 | | 176.99 | | 7.50 | |
| Survey area (n mile$^2$) | 10575 | | 2100 | | 2100 | | 10575 | |
| Survey area ($A$, × 10$^6$ m$^2$) | 36271 | | 7203 | | 7203 | | 36271 | |
| Biomass ($B$, × 10$^3$ t) | 2220 | | 729 | | 424 | | 1075 | |
| CV (%) | 15.75 | | 22.22 | | 22.59 | | 9.25 | |

Foote et al. (1990) noted that abundance estimates of krill using acoustics were often much less than those obtained from estimates of predator demand. They suspected large errors associated with the definition of individual krill target strength, and ensonified live krill aggregations in a cage at 120 kHz. The mean single-animal target strength of 30 to 39 mm krill was inferred from the aggregation backscatter to range from −81 to −74 dB. Everson et al. (1990) noted that these values were considerably lower that those calculated from previously used equations relating target strength to the physical size of krill (BIOMASS 1986), and that the use of these equations resulted in gross underestimates of krill abundance. Until recently, a fluid sphere model was used to characterize the target strength of krill. Wiebe et al. (1990) ensonified several species of live, but tethered, zooplankton at 420 kHz and concluded that sound scatter from elongated animals is better described by a bent cylinder model (Stanton 1989), and that target strength is proportional to the volume of an animal rather than its cross-sectional area. Using these data, Greene et al. (1991) predicted krill target strength at several frequencies and over a range of body lengths. The Foote et al. (1990) data agreed with the Greene et al. (1991) prediction. Further corroboration was offered by Hewitt & Demer (1991) who reported a set of *in situ* target strength measurements using a 120 kHz split-beam transducer. For krill with an estimated mean length of 47.4 mm, the modal target strength was −69 dB, within 1 dB of the prediction by Greene et al. (1991). The CCAMLR Working Group on Krill reviewed these and several unpublished studies on krill target strength and concluded that 'a growing body of evidence suggests that the BIOMASS definition of target strength as a function of body length at 120 kHz consistently overestimates target strength', and that 'measurements over a range of animal lengths imply a stronger dependence of target strength on length than that predicted by the BIOMASS definition' (SC-CAMLR-X 1991). Although the Greene et al. (1991) equation is a currently accepted estimator of krill target strength, body shape, orientation and physical condition also affect target strength (Stanton 1989). The range of variation of these parameters should be measured under conditions when the krill would be surveyed, and used in theoretical models to predict the distribution of individual target strengths that would be expected from a natural aggregation of krill (SC-CAMLR-X 1991).

Estimates of krill biomass density are insensitive to minor variations in the frequency distribution of length. This is because the number of krill per kg

Table 2. *Euphausia superba*. Krill weight, numbers per kg, target strength (*TS*) per individual, *TS* per kg, backscattering cross-section per kg, and kg per backscattering cross-section by standard length

| A<br>Length<br>(mm) | B<br>Wet wt<br>(g) | C<br>No. of krill $kg^{-1}$ | D<br>*TS* $ind.^{-1}$<br>(dB) | E<br>*TS* $kg^{-1}$<br>(dB) | F<br>Backscattering cross-sectional area of 1 kg krill ($m^2$ $kg^{-1}$) | G<br>kg krill $m^{-2}$ backscattering area (kg $m^{-2}$) |
|---|---|---|---|---|---|---|
| 20 | 0.0409 | 24463 | −82.11 | −38.22 | 0.001892 | 529 |
| 25 | 0.0858 | 11649 | −78.73 | −38.07 | 0.001960 | 510 |
| 30 | 0.1574 | 6354 | −75.97 | −37.94 | 0.002018 | 495 |
| 35 | 0.2628 | 3806 | −73.64 | −37.84 | 0.002069 | 483 |
| 40 | 0.4096 | 2441 | −71.62 | −37.74 | 0.002113 | 473 |
| 45 | 0.6060 | 1650 | −69.84 | −37.66 | 0.002154 | 464 |
| 50 | 0.8603 | 1162 | −68.24 | −37.59 | 0.002190 | 457 |
| 55 | 1.1810 | 847 | −66.80 | −37.52 | 0.002224 | 450 |
| 60 | 1.5773 | 634 | −65.48 | −37.46 | 0.002255 | 443 |

$B = (0.00193\ A^{3.325})/1000$

$C = 1000/B$

$D = -127.45 - 34.85 \log(A)$

$E = 10 \log(C) + D$

$F = 4\pi 10^{E/10}$

$G = 1/E$

decreases exponentially with increasing length at approximately the same rate as the backscattering cross-sectional area of a single krill increases with increasing length. The dependence of weight, numbers per kg, target strength per individual, target strength per kg, backscattering cross-sectional area per kg and kg per $m^2$ of backscattering area on standard length are illustrated in Table 2 and Fig. 7a to e. As can be seen from Table 2, the factor relating krill biomass to backscattering area varies from 529 to 443 kg $m^{-2}$ of backscattering area over a range of krill lengths from 20 to 60 mm. This implies that mean length may be used to calculate biomass densities without introducing substantial errors. If, on the other hand, numerical densities are desired (e.g. for studies of foraging behavior) then body length is critical to accurate estimates.

Species identification is problematic. Several high-resolution Multiple Opening-Closing Net and Environmental Sampling System (MOCNESS) tows were aimed at specific echogram types. Swarming krill appear quite different from the other major sources of zooplankton sound scattering (other euphausids, primarily *Thysanoessa macrura*; amphipods, primarily *Themisto gaudichaudii*; copepods; and salps): the edges of krill swarms, although irregular, are very sharp and distinct, and the volume backscattering strength of krill aggregations is much higher than that for other taxa. Although the total number of non-krill zooplankton caught in the IKMT tows exceeded that of

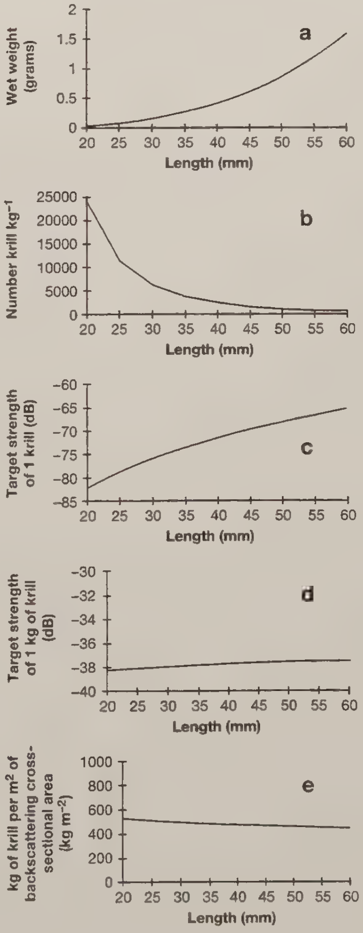

Fig. 7. *Euphausia superba*. Dependence of (a) krill weight, (b) numbers per kg, (c) target strength per individual, (d) target strength per kg, and (e) kg per backscattering cross-section, on standard length

krill (Loeb et al. 1992), their aggregate backscattering strength, estimated by assuming that target strength of elongated zooplankton is proportional to the cube of their length (Wiebe et al. 1990), was less than 10 % of that from krill over the survey area. Backscattering from krill and non-krill zooplankton were lumped together and biomass estimates are thus biased slightly upward. Although *Salpa thompsoni* were the most abundant non-krill zooplankton, they were not included in the above calculation because as gelatinous tunicates they are unlike any taxa included in Wiebe et al. (1990) experiments. Because they are mostly water and lack a strong density contrast, salps are probably not efficient sound scatterers. Although the numerical density of salps was higher than that of krill in IKMT samples collected in the southern and eastern portions of the large-area surveys, the integrated backscattering strength in these areas was low.

Krill within 10 m of the surface, below 250 m, and more dispersed than a threshold density of approximately 0.1 krill $m^{-3}$ were not detected and thus not included in the biomass estimates. Survey effort was not adjusted for the time of day so that the amount of undetected krill could have varied with diel changes in krill behavior. Ship's position was independent of time of day, however, and any diel effects should be random error added to the estimate of systematic bias caused by undetected krill. There were occasions when surface swarms were observed during daylight hours; and krill were sometimes entrained in the ship's cooling water intake during the day, although more frequently at night. The amount of krill in the upper 10 m, however, can be a substantial, but unknown, portion of that in the entire water column, and a potentially large source of error. This region could be investigated by using side-looking and up-looking transducers. In their review, Miller & Hampton (1989) note that krill are principally found in the upper 150 m of the water column. The lack of evidence to the contrary, however, does not preclude substantial numbers of krill below 250 m depth. Lower frequency echo sounders, acoustic transducers mounted on remote vehicles, and/or deeper fishing nets could be used to detect krill deeper than 250 m. The maximum density of undetected dispersed krill, assuming a density of 0.1 krill $m^{-3}$ throughout the upper 250 m and an average individual weight of 0.5 g, is less than 10 % of the average density of the 4 surveys. It is very unlikely that undetected krill would be present throughout the water column at just below the threshold density, and thus errors due to non-detection of dispersed krill are considered negligible.

Foote (1983) demonstrated that it was reasonable to assume that volume backscattering strength from fish schools was the result of incoherent addition of echoes from individual fish within the sample volume. The linear relationship between backscattering strength and density breaks down, however, at very high animal densities due to the effects of shadowing and multiple scattering (MacLennan & Simmonds 1992). Although peak $s_V$ values indicated krill densities on the order of $10^3$ ind. $m^{-3}$, shadowing may have occurred, particulary with thick swarms and layers. Evidence of multiple scattering was observed occasionally in association with very dense swarms. This ringing, observed as diffuse echoes below the more solid return from the swarm, was included in the integration with the expectation that multiple scattering helps offset the effect of shadowing (Stanton 1983).

Calibration inaccuracies can also contribute to the error in integration survey results. Foote & MacLennan (1984) stated that precision calibration to within 0.5 dB is possible by using standard calibration spheres. This translates to a 1 dB error in estimating mean target strength. Robinson (1984) noted that the acoustic absorption coefficient at 120 kHz is not known better than ± 0.5 dB $km^{-1}$. This implies that, at a range of 50 m, calibration accuracy can be no better than ± 0.5 dB due to this parameter alone. Our calibration experiments using various pulse lengths and sphere materials indicated system gain variations of as much as 1.2 and 1.5 dB, respectively (Demer & Hewitt in press).

Application of Jolly & Hampton's (1990) formula for estimating variance is valid only if the parallel survey transects are randomly spaced. Because the intent was to derive distribution maps as well as estimate abundance, transects were regularly spaced and Jolly & Hampton's expression for variance was used as an approximation. As such it is an underestimate of the true survey sampling variance.

The range of estimates of krill abundance in the Elephant Island area reported here is within the range of previously reported values. Macaulay et al. (1984) estimated that 2.1 million t of krill were aggregated in a large swarm located over the shelf break north of Elephant Island. Acoustic surveys conducted by Macaulay in the austral summers of 1981, 1984, 1987, 1988 and 1989, when normalized to a survey area of 5055 n $mile^2$ centered on Elephant Island, resulted in biomass estimates of 0.8, 0.3, 0.7, 0.5 and 0.9 million t respectively (Macaulay unpubl.). Macaulay (pers. comm.) assumed the target strength of 40 to 45 mm krill to be −35.93 dB $kg^{-1}$; incorporating the more recent definition of krill target strength (−37.70 dB $kg^{-1}$, Table 2) results in adjusted biomass estimates of 1.2, 0.4, 1.0, 0.7 and 1.4 million t. Klindt (1986) reported biomass estimates from combined acoustic and net surveys conducted in the Elephant Island area during 1983, 1984 and 1985 of 0.05, 0.4 and 0.02 million t respectively. Klindt used the BIOMASS (1984) definition

Table 3. *Euphausia superba*. Acoustic estimates of krill biomass in the Elephant Island area

| Year | Month | Survey area (n mile$^2$) | Biomass ($\times 10^3$ t) | Adj. biomass ($\times 10^3$ t) | Source |
|---|---|---|---|---|---|
| 1981 | March | 5055 | 790[a] | 1187 | Macaulay (unpubl.) |
| 1983 | October/November | 10507 | 52 | 480 | Klindt (1986) |
| 1984 | March | 5055 | 260 | 390 | Macaulay (unpubl.) |
| 1984 | November/December | 10106 | 380 | 2200 | Klindt (1986) |
| 1985 | March/April | 9283 | 16 | 81 | Klindt (1986) |
| 1987 | January | 5055 | 660 | 992 | Macaulay (unpubl.) |
| 1988 | January | 5055 | 480 | 721 | Macaulay (unpubl.) |
| 1989 | February | 5055 | 950[a] | 1428 | Macaulay (unpubl.) |
| 1990 | Early January | 11925 | 465 | 699 | Amos et al. (1990) |
|  | Late January | 10575 | 1132 | 1702 | Amos et al. (1990) |
|  | Early February | 11925 | 2133 | 3206 | Amos et al. (1990) |
|  | Late February | 11925 | 2475 | 3720 | Amos et al. (1990) |
| 1991 | Late January | 12675 | 689 | 1036 | Macaulay & Mathisen (1991) |
|  | Late Feb. – early Mar. | 12525 | 822 | 1236 | Macaulay & Mathisen (1991) |
| 1992 | Late January | 10575 | 2220 | 2220 | This report |
|  | Early March | 10575 | 1075 | 1075 | This report |

[a] Excluding biomass of observed superswarms

of target strength adjusted to 150 kHz and the length frequency distributions reported by Siegel (1986a). Klindt's biomass estimates may be adjusted by a factor corresponding to the difference in target strength at 120 kHz using the modal krill lengths for each of the surveys (30, 41 and 45 mm); the corresponding factors (9.2, 5.8 and 4.9) result in adjusted biomass estimates of 0.5, 2.2 and 0.1 million t. Four surveys were conducted by Macaulay in the Elephant Island area during January and February 1990 (Amos et al. 1990). Estimated krill biomass increased from the first survey through the fourth survey (0.5, 1.1, 2.1 and 2.4 million t). Two surveys were conducted by Macaulay between mid-January and mid-February 1991 (Macaulay & Mathisen 1991). Estimated krill biomass increased from 0.7 to 0.8 million t. For the 1990 and 1991 surveys, Macaulay (pers. comm.) again used $-35.93$ dB kg$^{-1}$ to scale his biomass estimates; adjusted biomass estimates are 0.7, 1.7, 3.2 and 3.7 million t for 1990, and 1.0 and 1.2 million t for 1991. Results from the above surveys are summarized in Table 3.

Krill abundance in the Elephant Island area decreased over the 2 mo observational period of mid-January to mid-March 1992. Krill abundance decreased approximately 2-fold between the 2 large-area surveys, Surveys A and D, conducted in the waters surrounding Elephant Island. Krill abundance also decreased approximately 2-fold between the 2 small-area surveys conducted to the north of Elephant Island, Surveys B and C. This was in marked contrast to the results from surveys conducted in 1990 and 1991 when krill abundance increased from mid-January to mid-March.

Over the last 3 yr, several measures of reproductive success of chinstrap penguins *Pygoscelis antarctica* at Seal Island varied in concert with estimates of krill biomass: moderately high in 1990, very low in 1991, and very high in 1992 (D. A. Croll pers. comm.). Seasonal variations in the availability of krill to predators may also be important. Although average abundances of krill during the 1990 and 1992 austral summer were similar, the seasonal timing of peak abundance was quite different – late in 1990, early in 1992. Reproductive success of chinstrap penguins was high in 1992 relative to 1990. Good breeding success early in the 1992 season, however, may be countered by the lack of krill late in the season when local demand for prey by newly fledged chicks and adults about to molt may be at its highest (Croll in press).

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# Age-specific mortality and transport of larval walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska

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ABSTRACT: A field study was conducted in May 1988 to estimate mortality rates of individual cohorts of larval walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Two surveys of the area of larval distribution were done 12 d apart and daily mortality rates estimated from changes in abundance of each cohort. This study was designed to minimize potential sources of bias to mortality estimates, such as larval extrusion or escapement from sampling gear, advective or diffusive gain or loss of larvae into or out of the sampling area, the uncertainty incurred by the use of length as a proxy for age, and the often erroneous assumption of constant production and mortality rates. The age-specific mortality rates from this study were low compared to rates previously estimated for larval walleye pollock. Four significant mortality estimates, ranging from 0.041 to 0.076 $d^{-1}$, came from among the youngest cohorts. The low larval mortality rates in 1988 coincided with very calm ocean conditions. Larval drift rates estimated in this study were coherent with the movement of a satellite-tracked drift buoy and averaged 3.1 to 3.9 cm $s^{-1}$, which is comparable to rates reported from other studies.

## INTRODUCTION

One of the most challenging problems in marine research is the estimation of mortality rates of organisms. This is particularly the case with planktonic early life stages of marine fishes due to the broad spatial and temporal scales of their distribution, their movement with currents, other sampling difficulties, and nonconstant birth rates (i.e. often peaked spawning cycles). It is frequently inappropriate to assume a stable age distribution and constant mortality rates to justify use of catch curve analysis (Ricker 1975, Hewitt & Methot 1982). Knowledge of mortality rates of marine fish eggs and larvae is a key to understanding the recruitment process of marine fishes because, for many species, the magnitude of recruitment may be established during early life stages (Houde 1987, Sundby et al. 1989, van der Veer et al. 1990). Accurate measurement of the magnitude and variability of mortality rates in the field is required to assess the causes and processes of mortality, such as predation and nutrition. Data on interannual variation in mortality rates can also be instrumental in forecasting year-class success.

We describe a method used to estimate the daily mortality rates for larval fishes from a population characterized by highly aggregated spawning that occurs over a short period of time. Walleye pollock *Theragra chalcogramma* spawning in Shelikof Strait (Alaska) occurs largely within a 1 mo period (Kim & Kendall 1989, Kendall & Picquelle 1990, Picquelle & Megrey in press). Larvae live in the upper 100 m of the water column and are advected to the southwest for several weeks in the Alaska Coastal Current (ACC) (Hinckley et al. 1990, Kendall & Picquelle 1990) and larval distributions are relatively predictable in time and space.

We have identified cohorts of larval walleye pollock from their hatch-date distributions as determined from daily growth increments on otoliths and have sampled

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the population twice, ca 12 d apart, to estimate mortality rates for each cohort. Larval transport was estimated from movement of several main patches of cohorts, from the displacement of centroids of the entire larval distribution, and from a satellite-tracked drift buoy (drogued at 40 m, the depth of highest larval abundance) released in the center of one of the main larval concentrations. Advection of larvae across the boundaries of the sampling grid was estimated from a model of advection and diffusion.

## METHODS

**Survey design.** Data from larval walleye pollock surveys of Shelikof Strait in 1986 and 1987 were examined to set the overall boundaries of the sampling area used in the present study and to estimate the likely abundances of larvae. An analysis of these data was used to estimate the number of stations needed to detect a reasonable minimum mortality rate. A power analysis (Zar 1984), using an estimate of variance of larval abundances in 1986 and 1987, indicated that, for a power of 0.8 and 0.95, a sample size of 50 stations per pass would detect overall mortality rates of 0.029 and 0.037 $d^{-1}$, respectively. These appeared to be reasonable lower limits of larval mortality which might be expected.

A stratified survey design was used for both passes. A stratification scheme for the first survey of the area (Pass 1) was based on prior information. Historically, high densities of larvae have been observed between Sutwik Island and the Semidi Islands (Fig. 1a). We also expected high densities in the inshore area north of Sutwik Island. Five strata were included in Pass 1 (Fig. 1a). The 7 strata for the second survey (Pass 2, Fig. 1b) were determined from the shipboard counts of the larvae found in Pass 1. The high inshore abundances found in Pass 1 were predicted to move to the southwest with the prevailing current; therefore the Pass 2 survey was extended further to the southwest.

The cruise was conducted from the NOAA vessel 'Miller Freeman' between 19 May and 9 June 1988. A grid of stations 9 or 19 km apart was established as described above and refined based on larval surveys of prior years, and from results of egg and larval cruises in April and May 1988. This grid was occupied from 21 to 24 May (Fig. 1a, Pass 1) and was resampled from 1 to 6 June (Fig. 1b, Pass 2). The mean date of each pass was separated by 12 d.

Three sets of gear comparisons were done – on 20 May, 30 May and 6 June – to examine catch rates by fish size for an estimate of larval escapement and avoidance of gear. The gears tested were a 60 cm bongo net with 0.333 mm mesh, a 1 m Tucker trawl with 0.505 mm mesh, a 3 m Tucker trawl with 1.5 mm mesh, and a Methot frame trawl with 2 × 3 mm oval mesh (Methot 1986). This range of gear types and mesh sizes has been shown to catch walleye pollock ranging from ca 4 to 40 mm standard length (SL) (M. Shima & K. Bailey unpubl.). Two daytime tows and 1 or 2 nighttime tows were done with each gear type. Each set of gear comparisons was located in an area of relatively high (>250 larvae 10 $m^{-2}$) abundance, and took ca 24 h to complete. All hauls for a particular set of gear comparisons were done at the same location.

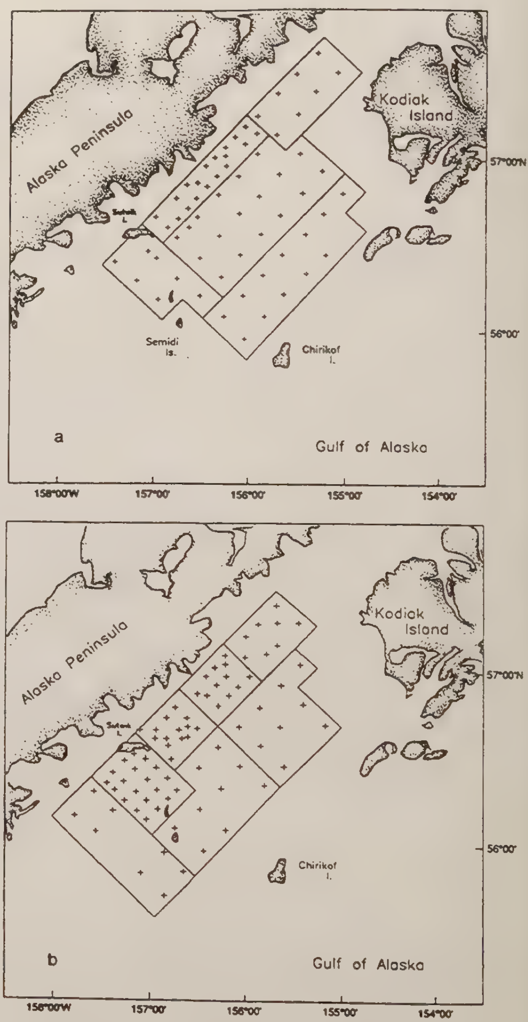


Fig. 1. Survey area for (a) Pass 1 and (b) Pass 2, including station locations and strata boundaries

The first set of gear comparison tows (20 May) indicated that the Tucker trawl was the most efficient in catching the size range of larvae observed (4 to 15 mm SL). It was therefore chosen as the standard gear for the larval surveys. Oblique tows were done to a depth of 100 m, as prior work has shown that larvae are above 100 m at this time of year (Kendall et al. 1987). The ship's speed was approximately 2 to 2.5 knots. A flow meter was used to normalize catch for volume filtered. The Tucker trawl was deployed with the net closed, and a messenger was sent to open the net when it reached sampling depth. The net was then retrieved at 20 m $\text{min}^{-1}$.

A subsample of walleye pollock larvae was removed from the cod end and immediately preserved for special studies. This subsample included larvae which were preserved in 95 % ethanol for daily growth increment analysis. In order to find areas of high concentrations of larvae for further special studies and to find the boundaries of the larval distribution (to ensure that the complete larval distribution was sampled), a volumetric subsampling method was used on the remainder of the catch to estimate the total number of larvae. The remaining contents of the cod end, aside from larvae removed for special studies, were preserved in 5 % buffered formalin. These samples were later resorted for a final count of walleye pollock larvae, which included those that had been removed for special studies.

**Analytic methods.** The number of larvae per tow was converted to number of larvae per 10 $m^2$ using a standard haul factor (Smith & Richardson 1977). Total number of larvae per pass was the sum over all strata of the stratum mean multiplied by the area of the stratum.

***Gear comparisons:*** For each of the 3 sets of gear comparison tows, catch rates by larval size interval were compared among gear types to test whether significant numbers of small or large larvae were missed by the sampling gear, and to examine catching efficiency by larval size. The number of larvae per 10 $m^2$ per 1 mm SL interval for each of the gear comparison tows was averaged by gear type. A Kolmogorov-Smirnov test (K-S; Zar 1984) was done to assess the difference in catch rates between the bongo net and the 1 m Tucker trawl.

An analysis of variance (ANOVA) of 1 m Tucker trawl catches was done to test whether catch rates differed between day and night (indicating gear avoidance). The catch per 10 $m^2$ at each survey station was log-transformed to equalize the variance. The factors in the ANOVA were strata and day/night. Two strata from Pass 1 were excluded because they contained only stations done during the day.

***Length-frequency and shrinkage:*** The standard length of 50 walleye pollock larvae per haul (Passes 1 & 2) was measured from a combination of ethanol-preserved larvae, formalin-preserved larvae, and larvae measured before preservation. Larval lengths from each preservative type were combined in order to construct an unbiased length-frequency file. Biases by preservative type were due to selective removal of larvae (by size) for special studies. The number of larvae measured from each preservative type was proportional to the total number of larvae which had been placed in that preservative. Samples from each preservative type were random. Lengths of larvae from different preservative types were converted to fresh (pre-fixation) lengths using the following relationships:

$$(\textit{95\% ethanol})\ \text{Fresh length} = \frac{\text{Fixed length} - 0.349}{0.900},$$

and

$$(\textit{5\% formalin})\ \text{Fresh length} = \frac{\text{Fixed length} - 0.097}{0.900}.$$

These relationships were derived from experiments [in 1988 and other years; D. Seifert, Alaska Fisheries Science Center (AFSC), 7600 Sand Point Way NE, Seattle, WA 98115, USA, pers. comm.] where fresh length and preserved length were measured on the same fish. Converted lengths were combined into an overall length-frequency for each pass.

***Aging:*** Approximately 15 to 20 fish per station from about 15 stations per pass were aged from otoliths by enumerating daily growth increments (Yoklavich & Bailey 1990). Daily growth increments have been validated by laboratory studies for this species (Nishimura & Yamada 1984, Bailey & Stehr 1986). Growth was linear over the size range (4.7 to 18.2 mm) examined ($R^2 = 0.90$).

An analysis of covariance (ANCOVA) was done to test differences in growth over the study period and area. The ANCOVA included length as a dependent variable, stratum as a categorical variable, and age as the covariate, and included an age-stratum interaction term. The analysis showed that the slope of the age-length regression (over the common range, 5 to 18 mm) did not vary significantly among stations over the survey area ($p = 0.919$). Within each pass, pair-wise tests of the equality of the intercepts (using Bonferroni probabilities; Miller 1981) of the length-age regression among strata showed that within Pass 1, 4 of the 5 pairs of strata tested had the same intercept ($p > 0.05$), while 1 was statistically different ($p < 0.05$). However, this difference was small and we considered it insignificant. Within Pass 2, the intercepts were the same among strata. Growth rates within each pass were therefore treated as equal.

***Mortality estimation:*** An age-length key (Kimura 1977) was computed for each pass. There were 309 larvae aged from Pass 1 and 249 larvae aged from

Pass 2. The elements in each row ($q_{la}$) of the key are the proportion of fish in length interval $l$ that are age $a$, thus each row is the age distribution for the length interval. Each element in the matrix is used to estimate the proportion of length $l$ larvae in the population that are age $a$. Age and length intervals were chosen to cover the range of the aged larvae (length ranged from 3 to 22.5 mm, age ranged from 6 to 62 d). The interval size must be large enough to contain enough larvae in the sample to produce reliable estimates of the true proportions in the population. In this application, length intervals of 0.5 mm were used. Daily ages were desired, but this resulted in too many age intervals for the number of aged larvae, so age intervals of 3 d were used. Additionally, the use of age intervals less than 3 d would not be justified as the measurement error in the aging process was ±1 d.

An age-length key was used for this study rather than an estimated age-length relationship for converting length-frequencies into age-frequencies. This is necessary because fish of a specific cohort may be missing from the population but could be misidentified in the length composition due to the averaging effect of the model. An age-length key preserves the shape of the age distribution present in the aged subsample, which is assumed to be a precise representation of the true age distribution if the aged subsample is unbiased.

The standardized catch of larvae at each station was partitioned into 3 d cohorts based on the length distribution at the station and the appropriate age-length key. Cohorts were defined by the age of the larvae on the mean date of the pass. For example, the mean date for Pass 2 was day-of-the-year (DOY) 155, so a larva sampled on DOY 153 with an estimated age of 22 to 24 d would be assigned to the 24- to 26-d-old cohort, its age on DOY 155. This age adjustment for the day of sampling was necessary because the duration of each pass (5 d) was longer than the duration of a cohort (3 d).

The total number of larvae in each cohort for each pass was computed by summing the estimated cohort totals from each stratum. The cohort totals for each stratum were estimated by averaging the estimated number of larvae from each station in the cohort over stations, then multiplying the average by the total area of the stratum.

$$C_{ha} = \sum_{i} C_{hia}$$

$$C_{hia} = A_{hi} \sum_{j}^{N_{hi}} \frac{C_{hiaj}}{N_{hi}}$$

where $C_{ha}$ = estimated abundance of cohort $a$ in Pass $h$; $C_{hia}$ = estimated abundance of cohort $a$ in stratum $i$ in Pass $h$; $C_{hiaj}$ = estimated no. of larvae in cohort $a$ per 10 m$^2$ at station $j$ in stratum $i$ in Pass $h$; $A_{hi}$ = area of stratum $i$ in Pass $h$ in units of 10 m$^2$; and $N_{hi}$ = no. of stations in stratum $i$ in Pass $h$.

The variance of the estimated cohort totals has 2 components: the variability about the standardized catch sizes within each stratum and the uncertainty about the age distribution. This uncertainty is due to using an age-length key to estimate the age of the larvae rather than measuring the age of each larva directly. Kimura (1977) estimated variance of an age distribution from an age-length key; however, in the present application, the age distribution variance was complicated by the fact that a cohort is comprised of larvae from different age intervals corresponding to the different sampling dates. Therefore, an estimator for the variance about a total of a range of ages was used (S. J. Picquelle, ASFC, pers. comm.). Covariance between the estimates for a cohort from the 2 passes is assumed to be zero because these estimates are taken from 2 surveys which are statistically independent.

Mortality rates were estimated for each 3 d cohort that was present in both passes. Cohorts represented by very few fish in the age-length key (i.e. very young and very old fish) were dropped from the mortality analysis, as they were suspected of being underrepresented in the catch. The mean dates of the 2 passes were separated by 12 d. An exponential function was used to estimate cohort-specific mortality rates over the 12 d.

$$C_{2,a} = C_{1,a}\, e^{-z_a(t_2 - t_1)}$$

$$z_a = \frac{\ln(C_{1,a}) - \ln(C_{2,a})}{t_2 - t_1}$$

where $z_a$ = estimated instantaneous daily mortality rate for cohort $a$; $t_2 - t_1$ = time between passes (12 d); $C_{1,a}$ = estimated abundance of cohort $a$ in Pass 1; and $C_{2,a}$ = estimated abundance of cohort $a$ in Pass 2.

This model was also used to calculate the instantaneous daily mortality rate for the combined 10 April to 16 May cohorts.

The variance of the mortality rate was estimated using the delta method (Seber 1982).

$$Var(z_a) \approx \frac{1}{(t_2 - t_1)^2}\left[\frac{Var(C_{1,a})}{C_{1,a}^2} + \frac{Var(C_{2,a})}{C_{2,a}^2}\right]$$

where $Var(z_a)$ = approximate estimate of variance about the mortality rate for cohort $a$; and $Var(C_{h,a})$ = estimate of the variance about the estimated abundance of cohort $a$ in Pass $h$ (Picquelle pers. comm.).

The significance of the mortality coefficients could have been tested with a simple $t$-test, however, the variance of the mortality rate is an approximation. Therefore, the significance of the mortality rate was inferred through the use of a test of the difference in abundance of each cohort between Passes 1 & 2. This was a 2-tailed test where the variances of the abundances were not assumed to be equal and the critical value for the test was a weighted average (Sokal & Rohlf 1981).

Biases to the mortality estimates caused by advective transport into or out of the study area were examined by a model of advection and diffusion developed for this area (P. Stabeno & L. Incze, NOAA, Pacific Marine Environmental Laboratory (PMEL), 7600 Sand Point Way NE, Seattle, unpubl. data). The model is a 2-dimensional (depth-integrated) finite difference model with an imposed velocity field, that contains terms for larval mortality and age-dependence:

$$\frac{\partial C}{\partial t} = -U\frac{\partial C}{\partial x} - V\frac{\partial C}{\partial y} - K_H\left(\frac{\partial^2 C}{\partial x^2} + \frac{\partial^2 C}{\partial y^2}\right) - Q(a,x,y,t)$$

where $C$ = the depth-integrated concentration of larvae; $t$ = time; $U$ = cross-strait horizontal velocity; $x$ = cross-strait axis; $V$ = along-strait horizontal velocity; $y$ = along-strait axis; $K_H$ = horizontal coefficient of eddy diffusivity; $Q(a,x,y,t)$ = the larval source and sink term (i.e. hatching and mortality); and $a$ = larval age.

The concentration of larvae was assumed constant normal to the model boundaries [$C(x,y,t) = 0$]. The horizontal velocities and coefficient of eddy diffusivity (which is assumed constant) were determined using drift buoy and current meter data. The only biological input into this model was an age-dependent mortality which enters via the $Q(a,x,y,t)$ term.

Larval concentrations measured during Pass 1 were used as initial input to the model. The age-dependent mortality used was from Yoklavich & Bailey (1990). The model was run for 12 d with the mean observed current field (as derived from satellite-tracked buoys; P. Stabeno & R. Reed, NOAA, PMEL, unpubl. data). The percent of larvae expected in the region covered in Pass 2 was predicted from the model output. For the mortality estimation, survey boundaries for Pass 2 were adjusted to reflect the area where more than 95% of the larvae were predicted to be by the model 12 d after the mean date of Pass 1.

As an alternative, mortality rates derived from the age composition within each pass were also calculated via catch curve analysis (Ricker 1975) for comparison to those derived from the 2 passes. Assumptions made when using this method are that production of fish of all ages is constant, that mortality rate for all ages is also constant, and that all ages are equally vulnerable to sampling gear. Total mortality rates, over all ages, from the catch curves within each pass were calculated from a regression of log abundance on age:

$$\ln(C_{ha}) = \alpha_h - z_h t_a$$

where $C_{ha}$ = estimated abundance of cohort $a$ in Pass $h$; $t_a$ = age of cohort $a$; $\alpha_h$ = intercept for Pass $h$; $z_h$ = estimated instantaneous daily mortality rate for Pass $h$.

***Larval drift:*** Larval spatial distributions were contoured separately for each 3 d cohort for each pass. These plots were examined for patterns of distribution and for evidence that part of the larval distribution might have been missed in either Pass 1 or Pass 2 (indicated by high concentrations of larvae near the survey boundaries), thereby biasing the mortality estimates. Drift of larvae between Passes 1 & 2 was measured by assuming coherence of 3 major observed larval patch features, and by measuring the net movement of these patches between the passes.

Centroids, a measure of the center of mass of the larval distribution computed by using abundances at each station weighted by the locations of the stations (Kendall & Picquelle 1990), were calculated for all larvae from each pass. Centroid locations were corrected for irregular sampling distribution (with more stations in the inshore areas) by weighting each station location not only by larval density, but also by the area each station represented. Net displacement of the centroids of larval distribution was calculated for the interval between the 2 passes.

The 2 estimates of larval drift (from patch displacement and centroid displacement) were compared to the estimates of upper-water-column movement derived from a satellite-tracked drift buoy that was released in an area of larval concentration near the Alaska Peninsula during Pass 1.

## RESULTS

### Day/night catch comparison and catchability

Catch rates of walleye pollock larvae did not vary significantly between day and night (ANOVA, p = 0.56, Table 1). There was no consistent pattern of catch in the day or the night. The strata effect was highly significant (ANOVA, p = 0.0003, Table 1).

Table 1. Analysis of variance of log-transformed catch rates (no. of larvae $10\,m^{-2}$) of the 1 m Tucker trawl using strata and day/night as factors

| Source | df | Mean square | $F$ | p |
|---|---|---|---|---|
| Strata | 9 | 2.7509 | 3.89 | 0.0003 |
| Day/night | 1 | 0.2462 | 0.35 | 0.5562 |
| Interaction | 9 | 0.8936 | 1.26 | 0.2639 |
| Error | 112 | 0.7064 | | |

The catch rates of the bongo and the 1 m Tucker trawl did not differ significantly (K-S test, $p = 0.89$). Other work on catchability of larvae by these gear types (Shima & Bailey unpubl. data) has also shown no consistent pattern of differing efficiency over this larval size range. The gear comparison experiments showed that the 1 m Tucker trawl was effective in catching the entire length-range of larvae that were caught by the other gear (Fig. 2). The 3 m Tucker trawl and the Methot trawl caught less than the bongo and the 1 m Tucker because of their large mesh sizes. There were not significant numbers of smaller larvae in the 0.333 mm mesh bongo, or larger larvae in the larger mesh 3 m Tucker or Methot trawls. Therefore, no correction of abundance estimates for escapement or avoidance was made to the survey station catches made with the 1 m Tucker trawl.

### Model of advection and diffusion

Estimates of probable changes in larval distribution derived from the application of the advection and diffusion model resulted in dropping the 2 northernmost stations from the Pass 2 survey. Larvae found at these 2 stations would have been upstream of the survey area in Pass 1 and therefore would have been advected into the Pass 2 survey area. Otherwise, the boundaries for Pass 2 were not changed, as the model predicted that more than 95 % of the larvae found in Pass 1 would be found within the area covered during Pass 2.

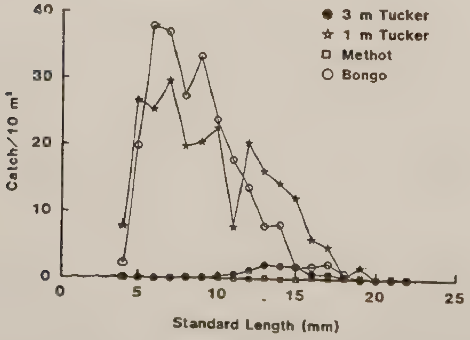


Fig. 2. *Theragra chalcogramma*. Comparison of catch at length of walleye pollock larvae averaged over all hauls from the 4 gear types

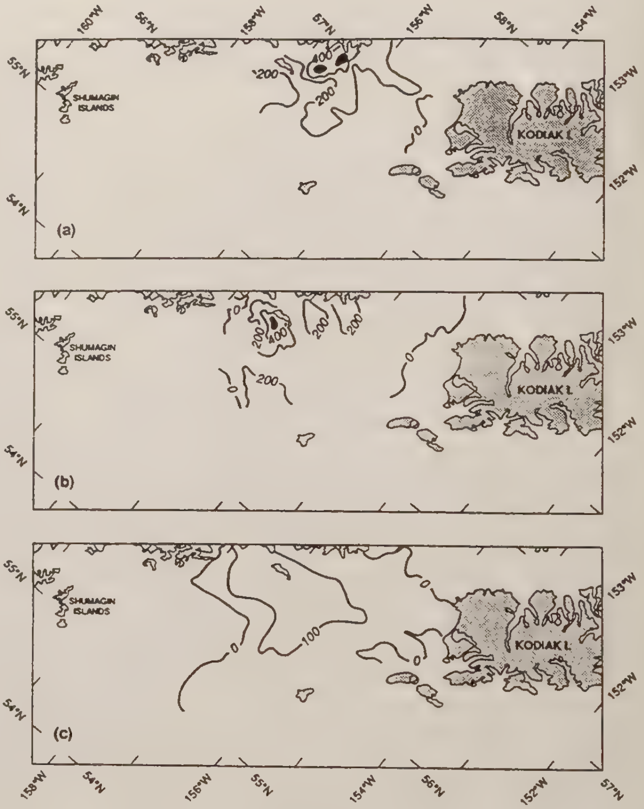


Fig. 3. The domain of the model is shown. Distribution of larvae (a) found during Pass 1 (this is the initial condition for the model), (b) found during Pass 2, and (c) predicted by the model of advection and diffusion for the time period corresponding to Pass 2. Larval abundance contours shown are ind. 10m$^{-2}$ (solid area: >600 larvae 10m$^{-2}$)

Comparison of the larval concentrations predicted from the model and those observed on the second survey (Fig. 3) shows that patch structure observed in the field was not preserved due to diffusion in the model, for all reasonable values of diffusivity ($K_H > 5 \times 10^5$ cm$^2$ s$^{-1}$).

### Mortality rates

Abundances of the 10 April through 16 May cohorts were used to estimate mortality rates. Abundances for the 10 through 28 April cohorts were very similar between Passes 1 & 2. Abundances of fish with hatch dates between 1 and 16 May showed a clear decline in abundance from the first to the second pass (Fig. 4).

The instantaneous daily mortality rates ($z$) for the separate 3 d cohorts ranged from −0.0574 to 0.0757 d$^{-1}$

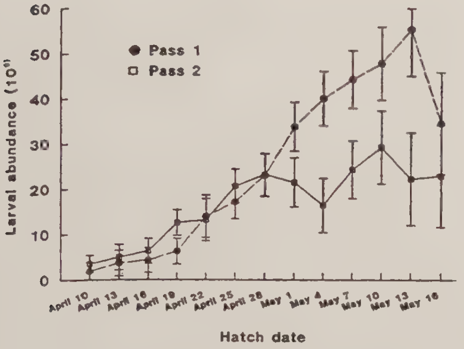


Fig. 4. *Theragra chalcogramma*. Larval abundance for 3 d cohorts during Passes 1 and 2

(Table 2). The instantaneous daily mortality rate for the combined 10 April to 16 May cohorts was $z = 0.033$ d$^{-1}$ ($Var(z) = 0.0013$). This mortality rate was not significantly different from zero ($t = 0.92$, $p > 0.20$).

Inspection of the cohort distributions for Pass 1 (Fig. 5) showed an area of relatively high concentration of larvae from the 10 to 19 April cohorts on the northwest side of the survey area near the Alaska Peninsula, which might not have been fully sampled. This was of interest due to the fact that the mortality rate estimated for these 4 cohorts were negative (Table 2). To test whether a significant number of larvae might have been missed in the inshore area during Pass 1 (which would have lowered the mortality rates for these cohorts), the northwest boundary of the survey area was redrawn closer to the Alaska Peninsula, increasing the total survey area for Pass 1. Larval abundances were extrapolated to the new boundary, and mortality rates recalculated using new total cohort abundances for Pass 1. The results of this analysis showed that, unless unusually high abundances of larvae were present in the nearshore areas outside the Pass 1 grid, extension of the survey area would not have been sufficient to raise the estimates of the mortality rates for these cohorts above zero (Table 3).

The overall daily mortality rate for each pass derived from the catch curve analysis was $z = 0.0838$ d$^{-1}$ for Pass 1, and $z = 0.0421$ d$^{-1}$ for Pass 2.

## Larval drift

Three main areas of concentration of larvae are visible in the distribution of the combined 10 April to 16 May cohorts in Pass 1 (Fig. 6a). Two patches were found to the northeast of Sutwik Island near the Alaska Peninsula ('Patch 1' and 'Patch 2'), and one was found to the northeast of the Semidi Islands ('Patch 3'). Three concentrations of larvae also are visible in Pass 2 (Fig. 6b), one to the northeast of Sutwik Island ('Patch 1'), one to the southwest of Sutwik Island ('Patch 2'), and one to the south of the Semidi Islands ('Patch 3'). Most of the 3 d cohorts were present in all 3 of these main patches in each pass.

There was an apparent southwestward displacement of all 3 patches over the interval between passes. By assuming the coherence of these 3 patches and measuring their displacement between the 2 passes, we could use their net movement over this time period as an estimate of the rate of larval drift. The time

Table 2. *Theragra chalcogramma*. Larval abundances and instantaneous daily mortality rates, $z$, (derived from 2 passes over the survey area) of 10 April to 16 May cohorts

| Hatch date | Age (d) | | Abundance of larvae in survey area | | | | $z$ (d$^{-1}$) | SE |
|---|---|---|---|---|---|---|---|---|
| | Pass 1 | Pass 2 | Pass 1 | | Pass 2 | | | |
| | | | Numbers | SE | Numbers | SE | | |
| 10 Apr | 42 | 54 | $1.971 \times 10^9$ | $1.891 \times 10^9$ | $3.564 \times 10^9$ | $2.569 \times 10^9$ | −0.0494 | 0.1000 |
| 13 Apr | 39 | 51 | $3.718 \times 10^9$ | $2.845 \times 10^9$ | $5.043 \times 10^9$ | $3.486 \times 10^9$ | −0.0254 | 0.0859 |
| 16 Apr | 36 | 48 | $4.381 \times 10^9$ | $2.749 \times 10^9$ | $6.365 \times 10^9$ | $3.191 \times 10^9$ | −0.0311 | 0.0669 |
| 19 Apr | 33 | 45 | $6.336 \times 10^9$ | $2.845 \times 10^9$ | $1.261 \times 10^{10}$ | $4.875 \times 10^9$ | −0.0574 | 0.0494 |
| 22 Apr | 30 | 42 | $1.400 \times 10^{10}$ | $4.656 \times 10^9$ | $1.322 \times 10^{10}$ | $4.128 \times 10^9$ | 0.0048 | 0.0380 |
| [illegible] Apr | 27 | 39 | $1.721 \times 10^{10}$ | $3.752 \times 10^9$ | $2.070 \times 10^{10}$ | $5.480 \times 10^9$ | −0.0154 | 0.0286 |
| 28 Apr | 24 | 36 | $2.308 \times 10^{10}$ | $4.712 \times 10^9$ | $2.323 \times 10^{10}$ | $5.631 \times 10^9$ | −0.0005 | 0.0264 |
| 1 May | 21 | 33 | $3.384 \times 10^{10}$ | $5.401 \times 10^9$ | $2.151 \times 10^{10}$ | $5.205 \times 10^9$ | 0.0377 | 0.0242 |
| 4 May | 18 | 30 | $4.008 \times 10^{10}$ | $5.991 \times 10^9$ | $1.646 \times 10^{10}$ | $4.018 \times 10^9$ | 0.0742 | 0.0239** |
| 7 May | 15 | 27 | $4.430 \times 10^{10}$ | $6.377 \times 10^9$ | $2.435 \times 10^{10}$ | $5.016 \times 10^9$ | 0.0499 | 0.0209** |
| 10 May | 12 | 24 | $4.788 \times 10^{10}$ | $8.078 \times 10^9$ | $2.930 \times 10^{10}$ | $6.166 \times 10^9$ | 0.0409 | 0.0225* |
| 13 May | 9 | 21 | $5.536 \times 10^{10}$ | $1.027 \times 10^{10}$ | $2.233 \times 10^{10}$ | $5.590 \times 10^9$ | 0.0757 | 0.0260** |
| 16 May | 6 | 18 | $3.466 \times 10^{10}$ | $1.130 \times 10^{10}$ | $2.296 \times 10^{10}$ | $6.020 \times 10^9$ | 0.0343 | 0.0349 |

*Significantly different from zero (α = 0.05)
**Significantly different from zero (α = 0.01)

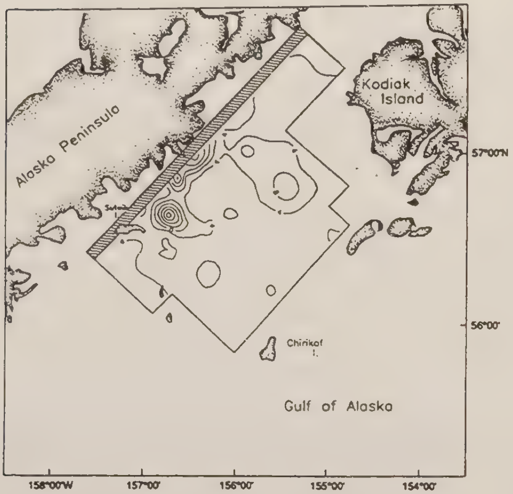


Fig. 5. *Theragra chalcogramma*. Distribution of the 19 April cohort during Pass 1 showing area on the northwest border of the survey area (shaded) where larvae might have been missed, causing underestimation of mortality rates. Larval abundance contours shown are ind. 10 $m^{-2}$

period over which movement was estimated was between the actual sampling dates at each patch rather than between the mean pass dates. Drift was calculated from the straight-line movement of patches between the 2 dates.

Patch 1 movement averaged 2.59 cm $s^{-1}$, Patch 2 averaged 3.61 cm $s^{-1}$, and Patch 3 averaged 5.29 cm $s^{-1}$. The average rate of drift for all 3 patches was 3.8 cm $s^{-1}$.

Rates of drift were also estimated from displacement of the centroids of the entire larval distributions for each pass. The location of the centroids for 1988 in Passes 1 & 2 were similar to 1981 and 1986 (Fig. 7). The centroid locations for 1979 and 1982 were further offshore. Centroid locations appear farther offshore than might be indicated by the distributions shown in the contour plots because the few high stations represented in the patches do not have a large impact on centroid locations, whereas they are interpolated over a larger area in the contour plots. The displacement of the centroids over the 12 d between mean pass dates suggests a rate of drift of 3.9 cm $s^{-1}$.

Table 3. *Theragra chalcogramma*. Results of increasing Pass 1 survey area on the northwest side of the grid and recalculation of daily mortality rates of the 10 to 19 April cohorts

| Hatch date | Mortality rate (uncorrected)[a] | Mortality rate (corrected)[b] | % Change in mortality rates |
|---|---|---|---|
| 10 Apr | −0.0494 | −0.0432 | +12.5 % |
| 13 Apr | −0.0254 | −0.0174 | +31.5 % |
| 16 Apr | −0.0311 | −0.0217 | +30.2 % |
| 19 Apr | −0.0574 | −0.0462 | +19.7 % |

[a] Using original Pass 1 survey boundary
[b] Using extended Pass 1 survey boundary

The net movement of the satellite-tracked buoy was compared to these 2 estimates of larval drift. The buoy was deployed on 24 May, near the center of Patch 1 (which was sampled at approximately this time) (Fig. 8). The buoy location on 31 May was close to the center of Patch 1 when it was sampled during Pass 2 (on 1 June). If only the period 24 May to 1 June was considered (corresponding approximately to the interval between the passes), the average velocity was 4.7 cm $s^{-1}$.

## DISCUSSION

Estimating larval mortality rates for marine fish is difficult due to the many sources of sampling bias and error. In this study, we have attempted to avoid many of the problems which have complicated earlier studies. Use of multiple surveys instead of the more usual catch curve analysis made it possible to avoid the assumptions of constant egg production and constant mortality. Comparisons of several gear types and day/night sampling indicated that retention and escapement of walleye pollock larvae from sampling gear was not a problem. Transport of larvae through the sampling area was accounted for by sampling virtually the entire distribution of walleye pollock larvae, and boundaries were refined through the use of a model of advection and diffusion developed for this area. By analyzing daily growth increments of otoliths, we avoided the uncertainty of using length as a proxy for age, ensured that the same cohorts were identified in each survey, and were able to estimate mortality rates for specific 3 d cohorts of larvae. Ageing also made it possible to truncate the range of cohorts that had estimated mortality rates to those that were adequately sampled in each pass. Also, Somerton & Koyabashi (1992) show that truncating the age distribution avoids bias due to low capture probabilities. Larvae hatched after completion of the first pass could also be excluded this way. Since virtually the complete vertical and horizontal distribution of larvae was sampled in this study, differences in spatial distribution of larvae, for example with age, were not a factor.

The range of mortality rates estimated from this study (−0.0574 to 0.0757) was low compared to other published mortality rates for walleye pollock during this developmental

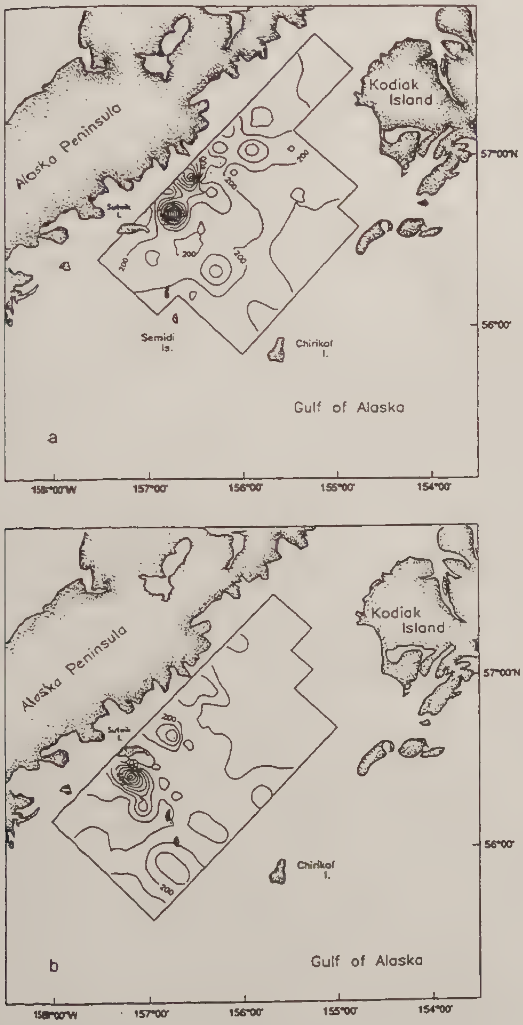


Fig. 6. *Theragra chalcogramma*. Distribution of 10 April to 1 May cohorts during (a) Pass 1 and (b) Pass 2. Larval abundance contours shown are ind. $10\,m^{-2}$

period. Rates from prior studies have ranged from $z$ = 0.065 to 0.11 $d^{-1}$ (Table 4). Estimates of mortality rates reported for the larval stage of other gadoids have also been also somewhat higher (e.g. for Atlantic cod: $z$ = 0.08 $d^{-1}$, Houde 1987; and $z$ = 0.12 $d^{-1}$, Sundby et al. 1989). The fact that the daily mortality rates for all of the 3 d cohorts were consistently low with none exceeding $z$ = 0.0747 $d^{-1}$ and that mortality rates determined from catch curve analysis were also low supports the conclusion that the low overall mortality rates found in this study were realistic.

In accordance with the low mortality rates observed for larvae, there is evidence that 1988 may be a relatively strong year-class for walleye pollock spawned in Shelikof Strait. There was a high relative abundance of 0-age juveniles caught in an August–September 1988 juvenile survey (Bailey & Spring 1992) indicating that recruitment was established early. Furthermore, the 1988 year-class has made a strong showing in the annual March hydroacoustic surveys of the Shelikof spawning stock in both 1990 and 1991 (Hollowed et al. 1991; J. Traynor, AFSC, pers. comm.). Low larval mortality rates during the spring of 1988 could have been a contributing factor to the strength of the year-class.

It is interesting to note that wind speeds during May of 1988 were much lower than normal for an extended period of time including the time period of this survey. The mean May wind speed (derived from atmospheric pressure gradients estimated from National Meteorological Center data) for 1988 was 4.63 m $s^{-1}$, whereas the average for May of 1980 to 1987 and 1989 was 6.70 m $s^{-1}$.) The mechanism explaining a relationship between wind speed and larval survival is not known, although several authors have speculated on possible causal relationships in other species (Lasker 1975, Sundby & Fossum 1989, MacKenzie & Leggett 1991).

Based on the power test done previously, we did not expect to resolve mortality rates below 0.037 $d^{-1}$ (for a power of 0.95). The 4 significant mortality rates were all greater than this (0.041 to 0.067 $d^{-1}$). Mortality rates of 9 of the 13 oldest cohorts were not significantly different from zero. There are several possible reasons for this. First, patchiness in the larval distribution could have caused the variance to be too large to make low mortality rates indistinguishable from zero. Better stratification and increased sampling in areas of high abundance could have reduced this source of variability. However, the patchy distribution of larvae and the uncertainty in predicting areas of high larval abundance make survey design difficult. Second, the fact that each pass was not synoptic (i.e. each took from 4 to 6 d to complete) and that the pass duration was greater than the duration (3 d) of each cohort caused an increase in the variance in the age-length key, as it was a composite from several days. Adding more passes and more days between the passes would be alternative ways to increase our ability to detect low rates of mortality. Third, there is high natural variation in the age-length relationship. A larger ageing sample would be helpful in reducing this source of variation. And fourth, although we tried to eliminate the possibility of advection of larvae into the survey area between Passes 1 & 2 through the survey design and use of the model of advection and diffusion, it is still possible that such immigration did occur.

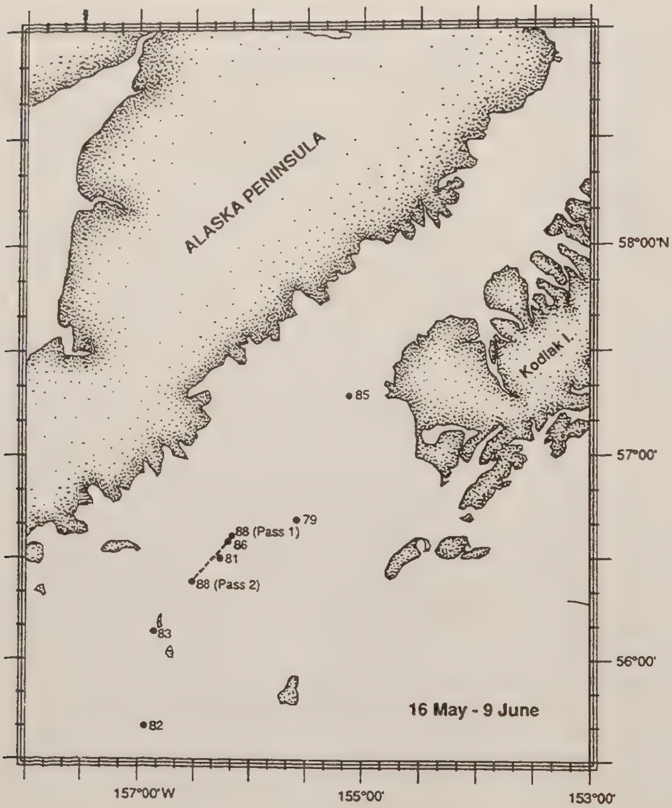


Fig. 7. *Theragra chalcogramma*. Centroids of larval distributions in Passes 1 and 2 (May 1988), as compared with other years (figure adapted from Kendall & Picquelle 1990)

Table 4. *Theragra chalcogramma*. Estimates of instantaneous daily mortality rates ($z$) for walleye pollock from Shelikof Strait from prior studies

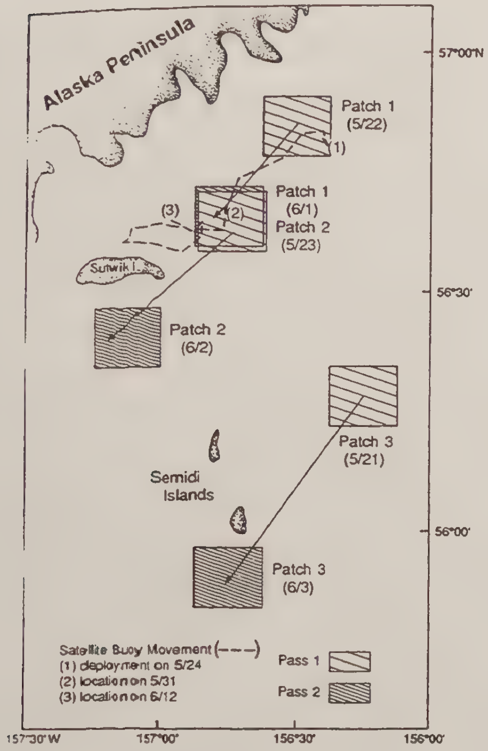
| Source | $z$ | Comments |
|---|---|---|
| Incze & Campbell (1989) | 0.11 | |
| Yoklavich & Bailey (1990) | 0.08 | Average of 4 to 65 d-old-larvae sampled in June |
| Kim (1987) | 0.096<br>0.082 | 4–5 mm cohort<br>8–9 mm cohort |
| Kim & Bang (1990) | 0.070 | |
| Kim & Gunderson (1989) | 0.086 | |
| Reed et al. (1989) | 0.065 | Within a larval patch |
| This study | 0.033<br>($Var(z) = 0.0013$) | For combined 10 Apr to 16 May cohorts |

It is interesting to note that the 4 significant mortality rates were for cohorts of young larvae. Mortality rates actually are probably higher for young fish. A decrease in mortality rate with age or size is to be expected (Cushing 1974), and has been reported for walleye pollock larvae by Yoklavich & Bailey (1990).

The mortality rates for the older cohorts were very low, and this, combined with very high variance, made them statistically indistinguishable from zero. The lack of significance of the mortality rates for older cohorts could also be explained by an underestimation of the abundance of older larvae during Pass 1 or an overestimation during Pass 2, either of which would have caused an apparent decrease in the mortality rate (or negative rates). There was no increase in the variance of the mortality rate relative to the mean with age, indicating that the distribution of older larvae was not patchier (which would have increased the variation in abundance estimates; Pielou 1977).

Transport of larvae was examined by displacement of larvae, by satellite drifter trajectories, and by satellite imagery. During the spring, daily mean current speeds in Shelikof Strait have been measured from 10 to 50 cm $s^{-1}$ (Schumacher et al. 1989); however, the current structure in Shelikof Strait is complex in both time and space (Stabeno & Incze unpubl.). Circulation is dominated by the Alaska Coastal Current (ACC), a narrow (less than 20 km wide), buoyancy-driven current system. There is much variability in current speeds and location and direction of the ACC within the study area (Reed et al. 1989). Eddy-like features on the order of 20 km in diameter are common and add complexity to the current structure. Due to the complex wind regime, regions of wind-driven convergence and divergence are common. Both eddies and regions of wind-generated convergence probably play a role in the observed patchiness of larvae.

Larval drift rates estimated by several different methods were all similar. The average drift rate from these 3 methods was ca 3.1 to 3.9 cm $s^{-1}$. This rate is comparable to the larval drift rates estimated from other studies for larval walleye pollock (Incze et al. 1989: about 4 cm $s^{-1}$; Kim & Kendall 1989: 3.2 cm $s^{-1}$; Reed et al. 1989: 5 cm $s^{-1}$; Kim & Bang 1990: 3.13 cm



*Theragra chalcogramma*. Boxes show the locations of the 3 main concentrations of larvae (as seen in Fig. 6a, b) and their net displacement between passes. The track of the satellite-tracked buoy is also shown

$s^{-1}$). Other studies have estimated transport rates as high as 8 to 9 cm $s^{-1}$ (Incze & Campbell 1989, Incze et al. 1990).

Daily average velocities usually are weak (<10 cm $s^{-1}$) in the region near Sutwik Island and the Semidi Islands, the areas where the larval patches were found for this study. This flow is not in the ACC where currents can be as fast as 50 cm $s^{-1}$. The low net drift of the larvae in the patches was small because they are not in the ACC. The model of advection and diffusion was able to retain larval patches if an eddy was included in the current field (Stabeno & Incze unpubl.). Both cyclonic and anticyclonic eddies have been observed in the Shelikof Strait region several times during the past 5 yr (Vastano et al. 1992, Schumacher et al. 1993, Stabeno & Incze unpubl.) and larval patches appear to be associated with these eddies.

Also, it is notable that there was no apparent along-strait gradient of ages with older larvae further downstream, as might be expected if all cohorts were spawned in the same location (Kim & Kendall 1989, Kendall & Picquelle 1990) and no mechanism for retention of cohorts was present.

Inferences can be made about the patterns and velocities of surface flow based on sea surface temperature (SST) pattern displacements derived from satellite images (Vastano & Borders 1984). A preliminary examination of SST patterns for the survey period in May of 1988 (A. C. Vastano, Dept. Oceanography, Texas A&M Univ., College Station, TX 77843, USA, pers. comm.) showed a circulatory feature to the northeast of the Semidi Islands on May 23 to 24 and another to the south of the Semidi Islands on June 4 to 5. The direction of flow between these 2 surface features would be consistent with the assumption of coherence between the larval patch feature found in this area. It is not clear from satellite images whether any circulatory features existed in the Sutwik Island area during our study that could have entrained the buoy and the larvae. The SST photographs do, however, indicate several significant meanders in the surface flow, particularly during the Pass 1 time period. The images also indicate a pattern of surface flow along the Alaska Peninsula near Sutwik Island in the same direction as the movement of the buoy and the inferred drift of Patches 1 & 2.

Larval patchiness may play a significant role in overall rates of larval mortality. Patch-level studies of larval growth, feeding and predation, and their importance to larval survival are being conducted for walleye pollock. The techniques described in this study will also continue to be used to obtain age-structured mortality rates, which, along with studies of the mechanisms and causes of larval mortality of walleye pollock in Shelikof Strait, will promote a better understanding of the dynamics of the recruitment process for this stock.

In summary, realistic and precise rates of larval pollock mortality were estimated for individual cohorts during the period of downstream drift in 1988. These estimates were low compared to those from other years, coinciding with calm ocean conditions during the larval drift period, and corresponding to relatively strong recruitment of the 1988 year class. These data reinforce the concept that good larval survival is a necessary, but perhaps not sufficient, factor for development of strong year-classes. Smaller and younger cohorts experienced significant mortality over the 12 d period between sampling dates, while mortality of older and larger cohorts was insignificant. The results support the concept of intra-specific size-dependent mortality.

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# Wounding in Hawaiian monk seals (*Monachus schauinslandi*)

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Injuries observed on endangered Hawaiian monk seals (*Monachus schauinslandi*) at Laysan Island and French Frigate Shoals in the northwestern Hawaiian Islands in 1988 and 1989 were classified into six major types, based on the source of the wounds: mating attempts by adult male monk seals; nonmating aggressive interactions with other seals; attacks by large sharks; attacks by cookiecutter sharks (*Isistius brasiliensis*); contact with coral reef or debris; and entanglement in netting or marine debris. At both locations, injuries inflicted by adult male seals during mobbing incidents, in which many males attempt to mate with one seal, were seen more frequently than other types of injuries in 1988 and 1989. Injury data from 1982–1987 at Laysan Island and from 1985–1989 at French Frigate Shoals were used to compare the distribution of mating injuries inflicted by adult males and injuries inflicted by large sharks over size and sex classes of seals. Mating injuries caused by adult male seals were seen primarily on adult females but were also seen on seals in other size classes. Mating injuries inflicted by adult males occurred earlier in the year and with greater frequency at Laysan Island than at French Frigate Shoals. Injuries inflicted by large sharks were observed more often on adult male seals than on seals in other size classes at Laysan Island; however, no such difference was seen among size classes at French Frigate Shoals.

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Les blessures observées chez le Phoque-moine d'Hawaii (*Monachus schauinslandi*), une espèce menacée, à l'île Laysan et sur les hauts-fonds French Frigate dans le nord-ouest de l'Archipel hawaïen en 1988 et 1989 ont pu être classifiées, d'après leur origine, en six catégories principales : aggressions des mâles adultes durant les tentatives d'accouplement, interactions aggressives non reliées à l'accouplement chez les autres phoques, attaques de grands requins, attaques du requin *Isistius brasiliensis*, contacts avec le récif ou les débris coralliens et empêtrements dans les filets de pêche ou autres agrès. Aux deux sites, c'étaient les blessures produites par les mâles adultes durant les cohues, lorsque plusieurs mâles cherchaient à s'accoupler avec une même femelle, qui étaient les plus fréquentes en 1988 et 1989. Des données récoltées en 1982–1987 à l'île Laysan et en 1985–1989 aux hauts-fonds French Frigate ont permis de comparer la répartition d'après la taille et le sexe des blessures infligées par les mâles durant l'accouplement et celles dues aux requins. Les blessures causées par les mâles durant l'accouplement se retrouvaient surtout chez les femelles adultes, mais aussi chez des phoques d'autres classes de taille; à l'île Laysan, ces blessures pouvaient s'observer plus fréquemment et plus tôt dans l'année qu'aux hauts-fonds French Frigate. Les blessures dues aux grands requins apparaissaient plus couramment sur les adultes mâles que sur les autres phoques à l'île Laysan, mais non aux hauts-fonds French Frigate.

[Traduit par la rédaction]

## Introduction

Injuries are generally considered detrimental to animals, for they can reduce the probability of survival (Congdon *et al.* 1974; Willis *et al.* 1982) or delay maturation (Maiorana 1977). Various types of scars and fresh injuries are seen on Hawaiian monk seals (*Monachus schauinslandi*) (Kenyon and Rice 1959; Wirtz 1968; Alcorn 1984; Johanos *et al.* 1987), but the different types have not been consistently described. Injuries to monk seals have received increased interest recently because they apparently have a detrimental effect on the reproduction and survival of individual seals, which in turn may negatively affect overall population growth and recovery of this endangered species (Gilmartin 1983). Consequently, it is important to describe and quantify the types of wounds to facilitate monitoring of their origin and frequency and to assess their significance to injured individuals as well as to the monk seal population as a whole.

Most injuries noted in the past have been attributed to attacks by sharks (e.g., Kenyon 1973) and to what has been termed "mobbing" behaviour of adult male monk seals (e.g., Alcorn 1984). Shark attack has been thought to be an important cause of mortality (Kenyon 1973). Although sharks have been observed to attack and feed upon monk seals (Balazs and Whittow 1979; Alcorn and Kam 1986), the extent to which shark predation affects the population is unknown. Mobbing behaviour involves many males trying to mate simultaneously with one female or subadult (male or female) seal (Johnson

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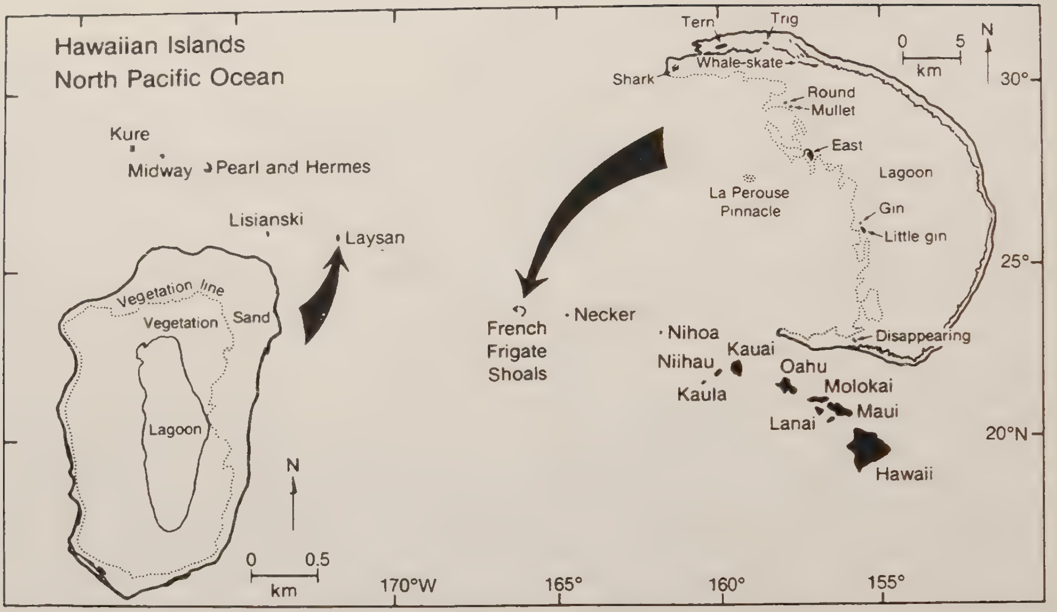

FIG. 1. Northwestern Hawaiian Islands, showing Laysan Island and French Frigate Shoals in detail. Note the difference in scale between Laysan Island and French Frigate Shoals.

and Johnson 1981; Johanos and Kam 1986; Johanos *et al.* 1987). During mating, the male mounts the female and bites her to hold his position on her back (Johanos *et al.* 1990). Puncture wounds and abrasions may be inflicted on the back of the female during mating. When more than one male tries to mate simultaneously with one seal, the biting becomes intense and harassment of the seal may continue over several hours, resulting in the formation and subsequent enlargement of open dorsal wounds (Johnson and Johnson 1981). In extreme cases the resulting wound may expose up to two-thirds of the dorsum (Alcorn 1984). Because of the apparent severity of such wounds, and of those inflicted by large sharks, the survival rate of wounded seals may be significantly lowered (Wirtz 1968; Johnson and Johnson 1981; Gilmartin 1983; Alcorn 1984).

In this paper we describe six major categories of injuries observed in two Hawaiian monk seal populations in the northwestern Hawaiian Islands during 1988 and 1989. Because wounds inflicted by adult male seals and by large sharks appear severe enough to affect the survival and reproduction of individuals, we examine the frequency of occurrence of these injuries in 1982–1989, and their possible effect on the monk seal population.

## Study sites and methods

Laysan Island (latitude 25°42′N, longitude 171°44′W; Fig. 1) is a low coral sand island about 2.8 km long and 1.7 km wide, with a hypersaline lake in its center. The island is surrounded by a fringing coral reef varying from 90 to 460 m in width (Ely and Clapp 1973). In 1989, when the entire monk seal population was identified, it consisted of 258 seals (excluding pups). The ratio of adult males to adult females was about 1.6:1 (Honolulu Laboratory, unpublished data).

French Frigate Shoals (FFS, latitude 23°45′N, longitude 166°10′W; Fig. 1) is a coral atoll with a crescent-shaped fringing reef, approximately 32 km long and 9.6 km wide, covering about 363 km$^2$ and containing 12 permanent sand islets, several sandspits that vary in size and location through the year, and one island of volcanic rock (Amerson 1971). The estimated monk seal population at FFS in 1988 was 623 animals (excluding pups). From beach counts, the ratio of adult males to adult females was estimated at 0.6:1 (Gilmartin *et al.* 1993).

We collected injury and census data on Hawaiian monk seals at Laysan Island during 28 February – 21 June 1988 and 28 March – 17 July 1989. At FFS, data were collected during 13 April – 30 August 1988 and 28 March – 3 September 1989. We also analyzed census and injury data collected in 1982–1987 at Laysan Island, and in 1985–1987 at FFS by Honolulu Laboratory personnel as part of an ongoing study of the population dynamics of Hawaiian monk seals.

At Laysan Island, adult and subadult seals were identified by means of numbers applied with commercial bleach (Stone 1984; all years except 1982, 1986, and 1987), distinctive scars, and natural markings. In addition, weaned pups were tagged with plastic Temple Tags (Gilmartin *et al.* 1986) each year beginning in 1983, and adult males were tagged from 1983 through 1988 (Johanos *et al.* 1987; Johanos and Austin 1988; Alcorn and Buelna 1989; Johanos *et al.* 1990). Seals with distinctive marks (e.g., large scars, flipper tags, or natural markings) were easily identified between years, but seals known only by marks applied with bleach were not consistently identified between years. At FFS, individuals were identified, when possible, by means of distinctive scars and natural markings. Temple Tags were applied to weaned pups beginning in 1984. No animals were marked with bleach and adult animals were not tagged during the study period.

Each seal was assigned to a size class on the basis of known age (e.g., nursing pup, weaned pup), reproductive state (adult female with nursing pup), or estimated size (juveniles, subadults, and adults), using criteria described in Stone (1984). The sex of a seal was recorded if seen, or if the seal had been previously identified and its

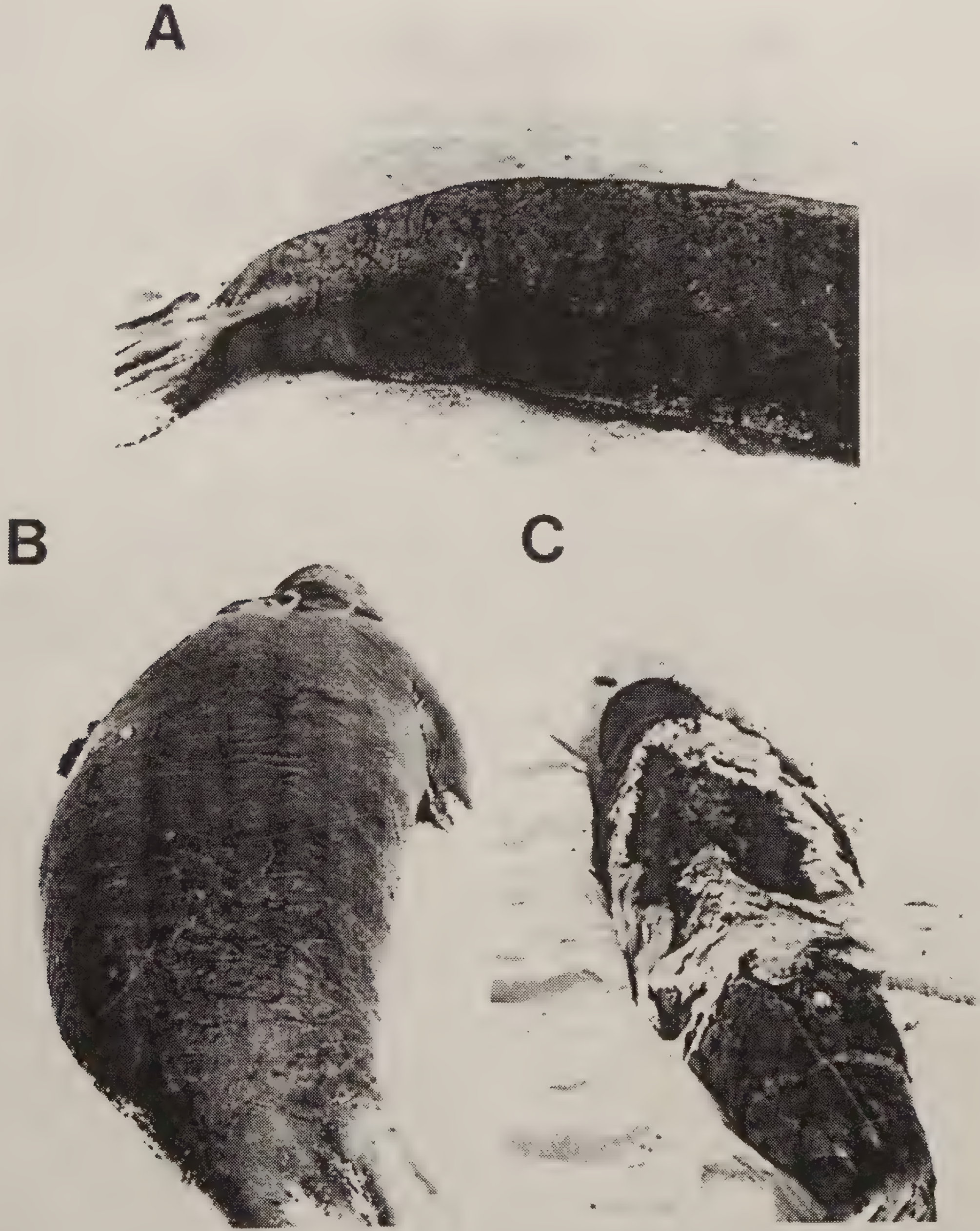

FIG. 2. Typical dorsal abrasions and lacerations (A and B) and gaping open dorsal injury (C) inflicted by adult male seals during mobbing incidents.

sex was known. An adult seal with a nursing pup was always classed as female.

The population composition was determined from daily census data. During censuses, all seals on land (with >50% of the body out of water) were counted as the observer walked around the perimeter of the island. On non-census days, less standardized observations were taken. Slightly different procedures were used at Laysan Island and FFS. At Laysan Island, censuses were conducted every 2–4 d, and took about 2.5 h to complete. Censuses at FFS were conducted every 1–2 weeks over a 2-d period. At islets too small for an

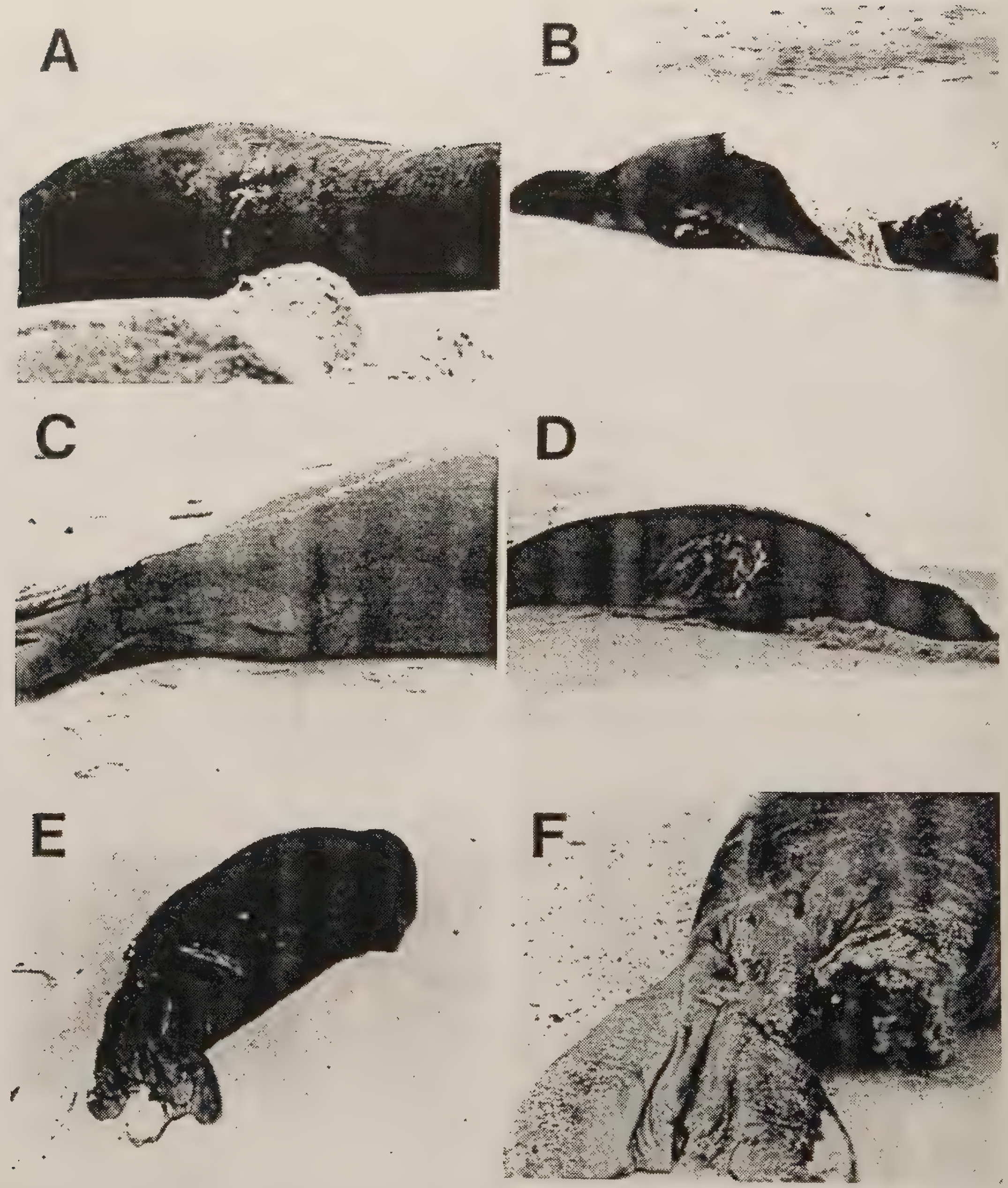

FIG. 3. Seal with a small open dorsal injury (A) and, about 10 days later, with a gaping open dorsal injury (B), both inflicted by adult male monk seals. (C) Seals with lacerations showing the shape of a shark's jaw. (D) A gaping injury showing the shape of a shark's jaw. (E) Fresh lacerations. (F) Seal with a hind flipper amputated.

observer to land without disturbing the seals, animals were counted from the boat.

Injuries were recorded both on census and non-census days. We standardized injury descriptions by grouping injuries into six types, based on physical characteristics: (1) *puncture*: small-diameter (<2 cm) hole, such as that created by a sharp pointed object piercing the skin; (2) *abcess*: a swollen, blister-like area under the skin; (3) *abrasions and lacerations*: scratches or tears in the skin ranging in depth from surface scratches (not breaking the skin) to deep tears in the muscle tissue; (4) *gaping wound*: an open, irregular- or oval-shaped wound

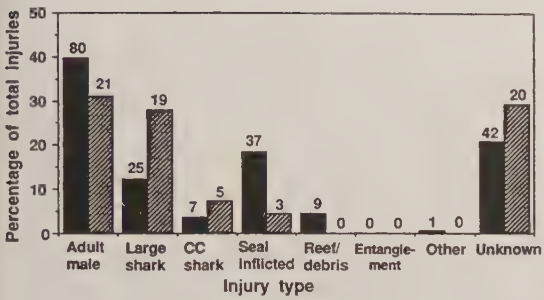

FIG. 4. Relative frequencies of different types of wounds observed on Hawaiian monk seals from April to June of 1988 and 1989 at Laysan Island (solid bars) and French Frigate Shoals (FFS) (hatched bars) in the northwestern Hawaiian Islands. See text for a description of wound types. The number of injuries of each type is indicated above each bar. "CC shark" indicates the cookiecutter shark (*Isistius brasiliensis*).

where flesh was removed; (5) *circular wound*: a wound ranging from a semicircular cut through the skin to a circular wound with flesh removed; (6) *amputation of a limb*: all or part of a limb removed from the body. Injuries recorded in 1988 and 1989 were classified by the observer. We classified injuries recorded by Honolulu Laboratory personnel from 1982 to 1987 by examining drawings and photographs taken at the time of observation. Each injury was used once in the analysis. If an animal was injured more than once during a season and the injuries were from a different source, the two injuries were counted separately.

### *Data analyses*

Only data from 1988 and 1989 were used to examine the frequency of occurrence of injuries from different sources because wounds were recorded more often and more systematically during those years. Data from all years (1982–1989) were used when examining injuries inflicted by adult male seals or by large sharks, as emphasis in data collection from 1982–1987 was placed on monitoring aggressive male behaviour and interactions between sharks and seals (e.g., Alcorn and Buelna 1989).

To minimize seasonal variation in censuses (Gerrodette 1985), we used the average number of seals counted in May and June of 1988 and 1989 as an index of the relative size of the population. To compare the monthly frequencies of occurrence of injuries inflicted by adult male seals and by large sharks between Laysan Island and FFS, we divided the monthly numbers of the two injury types by this index of population size.

To determine if data collected in 1988 and 1989 were similar to those collected in 1982–1987, we compared the two data sets (*G*-test; Sokal and Rohlf 1981). We pooled the data sets where no statistically significant differences were detected. All tests were evaluated at the 0.05 significance level.

## Results

### *Causes of injuries*

The shape of an injury and its location on the seal's body were often indicative of its origin. Six characteristic types of injuries, based on the cause of the wound, were observed.

### *Injuries inflicted by adult male monk seals during mating attempts*

Wounds inflicted by adult males during mating attempts consisted of abrasions on the dorsum of the injured seal, occasionally extending to its sides. The scratches were caused by an adult male attempting to hold the seal with its teeth and foreflippers while mounting it (Figs. 2A, 2B). Often the dorsum of the injured seal was dark because of subcutaneous hemorrhage (Alcorn 1984) and fluids leaching from the abrasions. Some seals also sustained more severe gaping wounds, usually in the midbody to posterior dorsal area. These gaping wounds ranged from small (ca. 2 cm diameter; Fig. 3A) to large open areas covering up to two-thirds of the injured animal's back (Figs. 2C, 3B; Alcorn 1984). In many cases the injured seal was observed with one or more adult males.

Mating injuries inflicted by adult males were the most frequently observed of all injuries at both Laysan Island and FFS (Fig. 4). These injuries were observed earlier in the year (April and May; Fig. 5), and the number of injuries (per 100 seals counted) inflicted was much higher at Laysan Island than at FFS. In June and July the rates from both areas were similar. At both Laysan Island and FFS the distribution of injuries inflicted by adult male seals over the size and sex classes of

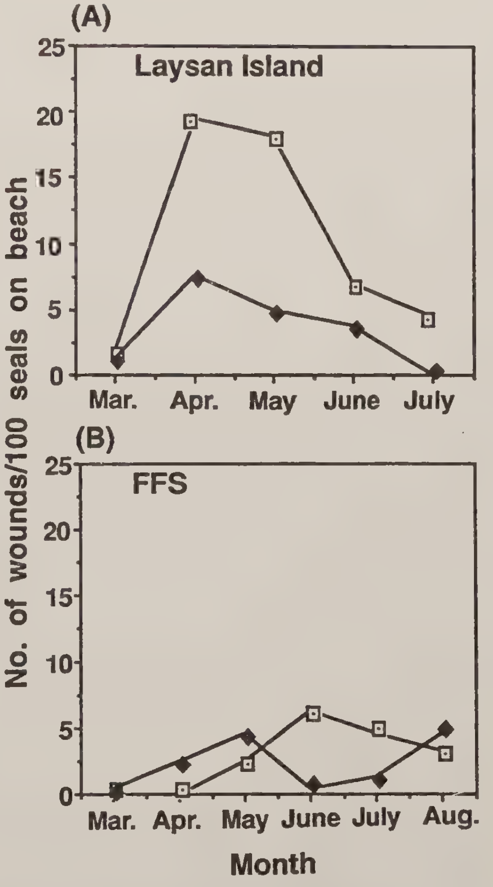

FIG. 5. Rate of wounding of Hawaiian monk seals by other adult male monk seals (⊡) and large sharks (♦) at Laysan Island (A) and French Frigate Shoals (B) in the northwestern Hawaiian Islands, 1988 and 1989. Seals of all size and sex classes are included.

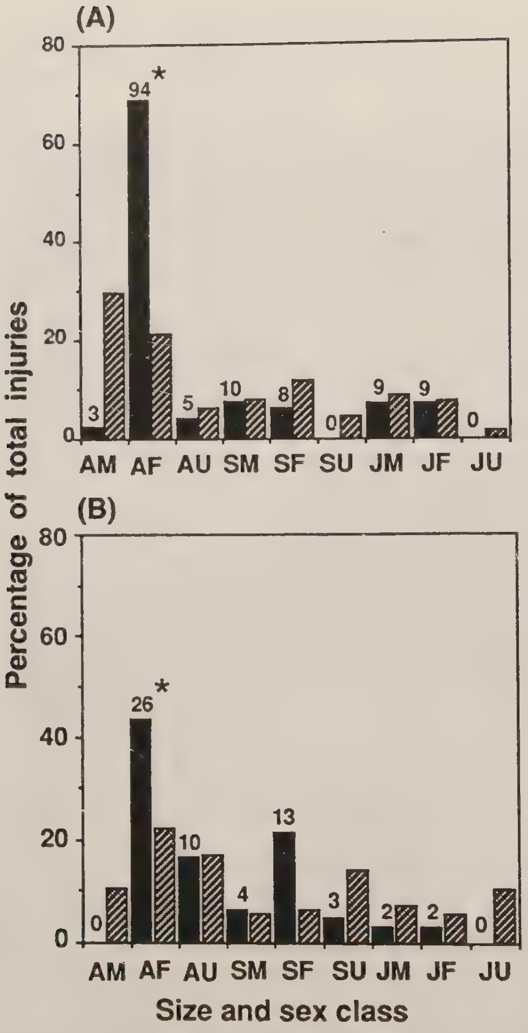

FIG. 6. Observed (solid bars) and expected (hatched bars) proportions of injuries inflicted by adult male Hawaiian monk seals on seals of different size and sex classes at Laysan Island (A) and French Frigate Shoals (B) in the northwestern Hawaiian Islands, 1982–1989. Expected frequencies are based on mean censuses in May and June of 1982–1989. The number of injuries in each class is indicated above each bar. AM, adult male; AF, adult female; AU, adult of unknown sex; SM, subadult male; SF, subadult female; SU, subadult of unknown sex; JM, juvenile male; JF, juvenile female; JU, juvenile of unknown sex. An asterisk indicates a significant difference between expected and observed proportions in a class.

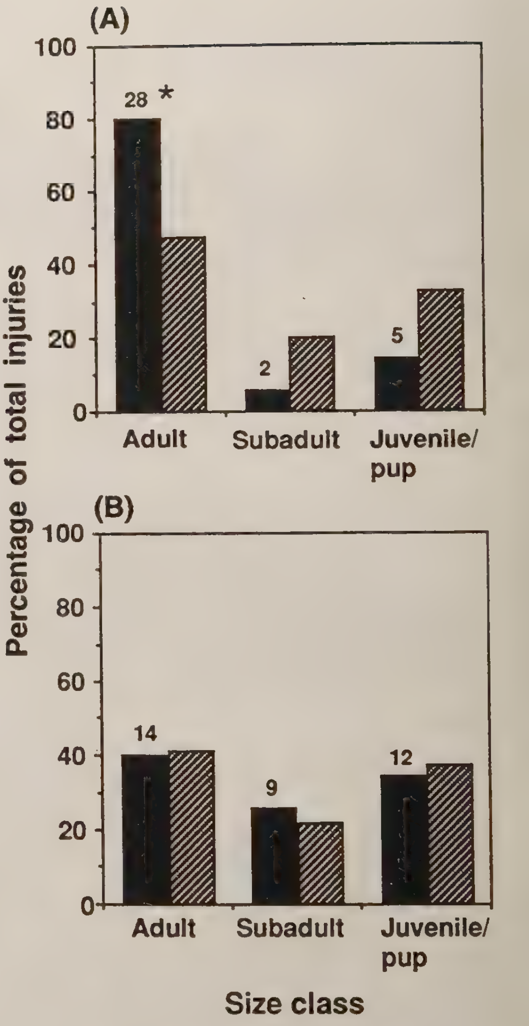

FIG. 7. Observed (solid bars) and expected (hatched bars) injuries inflicted by large sharks on Hawaiian monk seals of different size-classes at Laysan Island (A) and French Frigate Shoals (B) in the northwestern Hawaiian Islands, 1982–1989. Expected frequencies are based on mean censuses in May and June of 1982–1989. The number of injuries in each class is indicated above each bar. An asterisk indicates a significant difference between expected and observed proportions in a class.

monk seals was not directly proportional to the number of seals in each size and sex class counted on the beach (*G*-test with Williams' correction; Sokal and Rohlf 1981; Laysan: $G = 172.65$, df = 8, $p < 0.005$, Fig. 6A; FFS: $G = 53.38$, df = 8, $p < 0.005$, Fig. 6B; injured animals of unknown sex were excluded from the analysis). Significantly more adult females were injured at both Laysan Island and FFS than expected from their relative numbers in the population (Laysan: $G = 52.76$, df = 1, $p < 0.005$; FFS: $G = 7.48$, df = 1, $p < 0.01$). At FFS, the distribution of injuries inflicted by adult males over size and sex classes should be interpreted conservatively because adult females were more likely to be identified than adult males, therefore the expected numbers of adult males and females may have been biased in favour of females. Even so, the proportion of mating injuries inflicted by adult males on adult and subadult females was much higher than on any of the other size classes (Fig. 6B).

*Injuries inflicted by other seals during aggressive interactions*

Seals inflicted abrasions and bite wounds on each other during jousting interactions, where two seals lunge at one another with open mouths and occasionally bite each other (Kenyon and Rice 1959) around the head, neck, and hind flippers. Injuries due to aggressive interactions accounted for 18.4% of injuries seen at Laysan Island but only 4.4% of injuries at FFS. Of 37 injuries of this type at Laysan Island, adult male seals were injured significantly more often than seals of other size and sex classes ($n = 27$; $G = 23.52$, df = 1, $p < 0.005$). At FFS, two of the three seal-inflicted injuries were sustained by adult males.

*Injuries inflicted by large sharks*

Injuries inflicted by large sharks included shallow punctures in the skin, deep lacerations, gaping wounds, and amputated limbs (Figs. 3C–3F). The characteristic crescent shape of these wounds reflected the shape of a shark's jaw (Figs. 3C, 3D). Large sharks inflicted 12.4% of injuries observed at Laysan Island and 27.9% of those seen at FFS (Fig. 4).

The number of injuries inflicted by large sharks observed (per 100 seals) at Laysan Island was highest from April through June (Fig. 5). At FFS over the same period, the rate of shark-inflicted injuries observed per 100 seals varied, but was lower than at Laysan Island in most years.

At Laysan Island, injuries inflicted by large sharks were observed significantly more often on adult seals than on subadults and juveniles ($G = 15.83$, df = 2, $p < 0.005$, Fig. 7A), and were observed significantly more frequently on adult males than on seals of other size classes ($G = 15.95$, df = 1, $p < 0.005$). At FFS, the distribution of large shark inflicted injuries was independent of size class ($G = 0.369$, df = 2, $p > 0.9$; Fig. 7B). Adult males did not sustain a significantly greater proportion of injuries than expected ($G = 1.67$, df = 1, $0.5 < p < 0.1$).

*Injuries inflicted by cookiecutter sharks (*Isistius brasiliensis*)*

Injuries inflicted by cookiecutter sharks included circular or semicircular cuts through the skin or round, open wounds 3–7 cm in diameter and 1–2 cm in depth, sometimes with a circular plug of skin and tissue attached to the edge of the wound (Fig. 8A). These injuries were seen with greater frequency at Laysan Island than at FFS (Fig. 4).

*Injuries due to contact with coral reef or debris*

A seal sustained abrasions, close together and parallel to each other (Fig. 8B), and single scratches when it scraped past a coral reef or sharp pieces of metal or glass debris. These injuries were minor and not observed frequently at FFS (Fig. 4).

*Injuries due to entanglement in netting*

Injuries caused by entanglement in netting or marine debris were deep, linear wounds, usually around the neck of the animal (Fig. 8C).

*Other injuries and unknown causes*

Injuries due to known but infrequently seen causes were classed as "other." Any injuries for which the cause was uncertain were classed as "unknown." At both Laysan Island

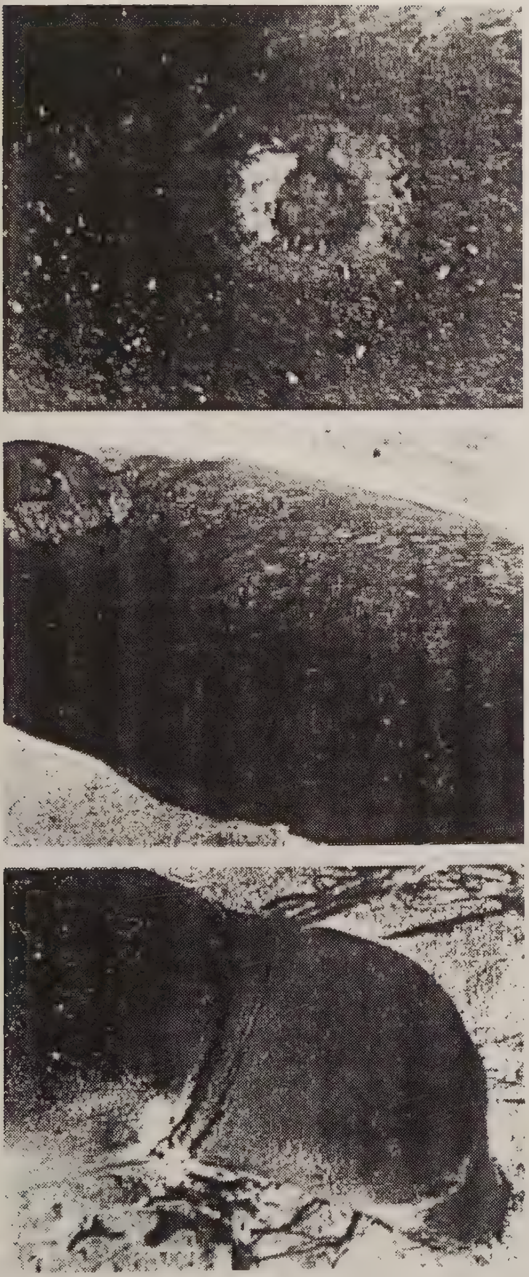

FIG. 8. Injuries observed on Hawaiian monk seals. (A) Round, crater-shaped wound caused by the cookiecutter shark (*Isistius brasiliensis*). (B) Parallel abrasions, close together, caused by contact with coral reef or debris. (C) Deep linear injury around neck of seal caused by a fishing net.

and FFS the proportion of injuries of unknown origin was high (20.9% at Laysan Island; 29.4% at FFS).

## Discussion

### *Injuries inflicted by adult males during mating incidents*

Mating injuries inflicted by adult males are likely to have a negative impact on the monk seal population because of their frequency (Fig. 4), severity (e.g., Figs. 2C, 3B), and occurrence mostly on female seals (Fig. 6; Hiruki *et al.*[2]). Although comparisons between Laysan Island and FFS should be interpreted cautiously, given the differences in frequency and methodology of seal counts at the two locations, the disparity in timing and rate of occurrence of adult male inflicted injuries is striking. Adult male inflicted injuries were observed earlier in the year and with 3–4 times greater incidence per 100 seals at Laysan Island than at FFS (Fig. 5). The higher frequency of such wounds at Laysan Island, combined with a small adult female population and increased female mortality due to injuries (Hiruki *et al.* 1993; Hiruki *et al.*[2]), suggest that wounding is likely to have a greater impact on the monk seal population at Laysan Island than on the population at FFS (Hiruki *et al.*[2]).

In other species, males also inflict injuries on females during courtship and mating, though the wounds may not be fatal. Male crabeater seals (*Lobodon carcinophagus*) usually bite the female on the neck while attempting to mount her (Siniff *et al.* 1979), resulting in considerable light wounding and superficial bleeding. Male southern elephant seals (*Mirounga leonina*) commonly inflict wounds on the female's neck during mating (McCann 1982). Male sea otters (*Enhydra lutris*) apparently infict wounds on the female during mating when the male takes a hold on the female's nose with his teeth (Foott 1970). Hatler (1972) found more serious wounds in a wild population of mink (*Mustela vison*) on Vancouver Island, where nearly every female mink observed during the mating season had extensive neck wounds.

Simultaneous pursuit of, and mating attempts with, a single female by many males, sometimes leading to injury or death of the female, is known in species other than the Hawaiian monk seal. Harassment of individual females by a group of males has been recorded for Australian sea lions (*Neophoca cinerea*; Marlow 1975) and southern sea lions (*Otario byronia*; Campagna and Le Boeuf 1988), where groups of subordinate males harass females as they arrive at or leave the breeding colony. Female northern elephant seals (*Mirounga angustirostris*), when harassed by groups of subordinate males, may sustain injuries serious enough to be fatal during mating (Le Boeuf and Mesnick 1990; Mesnick and Le Boeuf 1991). Groups of male manatees (*Trichechus manatus*) often pursue a single estrous female and attempt to copulate with her (Hartman 1979). Female dugongs (*Dugong dugon*) are frequently scarred by males attempting to mate with them (Anderson and Birtles 1978) and are sometimes mounted by several males until the female "appears very tired" (Preen 1989). A female mink can die from neck injuries that become enlarged when several males mate with her over a short period of time (Hatler 1972). In many species of waterfowl, forced extra-pair copulatory behaviour, in which one or several males pursue and attempt to mate with one female, has been widely documented (e.g., Titman and Lowther 1975; Bailey *et al.* 1978), and the female is occasionally killed during these incidents (McKinney *et al.* 1983). Female white-fronted bee-eaters (*Merops bullockoides*) are often chased by as many as 12 males during forced copulation attempts (Emlen and Wrege 1986). Female toads (*Bufo bufo*) and wood frogs (*Rana sylvatica*) involved in mating struggles in areas of high density may be drowned at the center of a ball of struggling males (Howard 1980; Arak 1983). Thus, the phenomenon of severe injuries inflicted on females by many males during the mating season is not unique to Hawaiian monk seals but is nevertheless important if the number of female seals is reduced as a result of mortality caused by these wounds, such as in the monk seal population at Laysan Island (Hiruki *et al.* 1993; Hiruki *et al.*, see footnote 2).

### *Injuries inflicted by seals during aggressive interactions*

The higher rate of injuries inflicted by seals during jousts or aggressive interactions at Laysan Island during 1988 and 1989 (Fig. 4) may indicate a higher level of intrasexual competition and aggressive behaviour between males at Laysan Island than at FFS. Males of many species often wound each other when competing for females (e.g., Weddell seals, *Leptonychotes weddelli*: Smith 1966; northern elephant seals: Le Boeuf 1974; Cox 1981; crabeater seals: Siniff *et al.* 1979; red deer, *Cervus elaphus*: Clutton-Brock *et al.* 1979; mule deer, *Odocoileus hemionus*, and white-tailed deer, *O. virginianus*: Geist 1986). In the context of males competing for females, other factors that may promote a higher level of aggressive behaviour at Laysan Island include its smaller size in comparison with FFS (Fig. 1), and the adult sex ratio at Laysan Island, which is skewed towards males. Deutsch (1985) found that Hawaiian monk seal males compete in two ways, as defined by Barash (1978): scramble competition, where a male searches for receptive females, and contest competition, where a male defends a female against intruding males. At Laysan Island, the distance a male must travel to find a receptive female is less than at FFS, suggesting that males at Laysan Island encounter receptive females, or males defending females, more frequently than at FFS. In addition, the greater number of males per female in the adult population at Laysan Island than at FFS implies that there are more contests between males for each female at Laysan Island. Thus, male monk seals at Laysan Island appear more likely than males at FFS to be involved in contests and aggressive interactions.

### *Injuries inflicted by large sharks*

Of the sharks commonly seen in the northwestern Hawaiian Islands (NWHI), tiger sharks (*Galeocerdo cuvier*) have the most potential to affect the monk seal population, as they are known to attack and eat monk seals (Taylor and Naftel 1978; Balazs and Whittow 1979; Alcorn and Kam 1986; B. L. Becker and L. M. Hiruki, personal observations). Hammerhead sharks (*Sphyrna lewini*) and mako sharks (*Isurus paucus*) have also been observed in the NWHI (Rice 1960), but there is no evidence that they attack monk seals. Although gray reef sharks (*Carcharhinus amblyrhynchos*) have not been observed to attack monk seals, they may be present when tiger sharks attack monk seals (Alcorn and Kam 1986).

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[2] L. M. Hiruki, I. Stirling, W. G. Gilmartin, B. L. Becker, and T. C. Johanos. Effects of wounding on monk seal (*Monachus schauinslandi*) population dynamics. Manuscript in preparation.

At Laysan Island, the larger proportion of injuries inflicted by sharks on adult monk seals than on seals of other size classes (Fig. 7A) may indicate either that juveniles are not injured by large sharks or, more likely, that juveniles are less likely to survive attacks by large sharks. Immature seals are generally considered to be more vulnerable to shark attack than adult seals (Le Boeuf *et al.* 1982; Brodie and Beck 1983; Ainley *et al.* 1985), perhaps because their lack of experience or smaller size makes them easier prey for sharks (Ainley *et al.* 1985). Both juvenile gray seals (*Halichoeurus grypus*; Brodie and Beck 1983) and juvenile bottlenose dolphins (*Tursiops truncatus*; Cockcroft *et al.* 1989) are relatively free of the scars typical of shark attacks, suggesting that they rarely escape when attacked by sharks. The predominance of young dolphin remains in shark stomachs also indicates that juveniles may be more vulnerable to shark attack than seals of other size classes (Cockcroft *et al.* 1989). If juvenile monk seals are less likely than adults to survive a shark attack, the effect of shark predation on juvenile seals may be greater than is indicated in Fig. 7.

Among adult seals, injuries inflicted by large sharks were observed more often on males than on females. Most of the injuries inflicted by large sharks were observed in April and May (Fig. 5), coinciding with the peak of the pupping season (Kenyon and Rice 1959; Kenyon 1981); however, as our observations did not extend past August, we have no data on the frequency of shark-inflicted injuries outside the pupping season. Nursing females stay on land or in shallow water until their pups are weaned (Kenyon and Rice 1959). During the same period, adult males spend most of their time in the water patrolling the shore and searching for receptive females. Thus, adult males may be more vulnerable than adult females to injury from sharks during the pupping season.

The decrease in the rate of wounding by sharks at both Laysan Island and FFS in June and July (Fig. 5) may have been due to tiger sharks shifting their focus to albatross chicks (*Diomedia* spp.). Tiger sharks begin to swim near the shore of several islands in the NWHI in mid-June, apparently to prey on albatross fledglings as they land in the water to rest between flights (Rice 1960; Johnson and Johnson 1981; W. R. Strong, personal communication). The seasonal predation on albatross chicks by tiger sharks in the NWHI may thus influence the frequency of shark attacks on monk seals (Rice 1960; Fisher 1975; W. R. Strong, personal communication).

### *Injuries inflicted by cookiecutter sharks*

The cookiecutter shark is a small squaloid shark, 14–50 cm long, that inhabits the deep (85–3500 m) water of tropical and subtropical areas of the Atlantic, Pacific, and Indian oceans (Castro 1983; Compagno 1984). Jones (1971) speculated that the bioluminescent pattern of the cookiecutter shark mimics that of a squid, and in doing so attracts squidophagous predators. Le Boeuf *et al.* (1987) view this as a likely explanation of how the cookiecutter shark attacks northern elephant seals. It is probable that Hawaiian monk seals are attacked in a similar way while feeding.

### *Interactions between wounding by adult male monk seals and by sharks*

At Laysan Island the rates of wounding by both adult male seals and large sharks were relatively high in April and May (Fig. 5). The overlap in peak periods of adult male inflicted mating injuries in shark-inflicted injuries may be related: body fluids leaching from a seal's injuries probably attract sharks, or a wounded seal may be less vigilant and less mobile in the water, both of which could increase its vulnerability to shark attack. Further, activity in the water can attract sharks; tiger sharks have been seen patrolling underneath aquatic mobbing incidents (Johanos and Austin 1988) and have subsequently attacked injured female seals (Alcorn and Kam 1986) as well as males involved in mobbing incidents (Johanos and Austin 1988). The combination of wounding by adult male monk seals and by sharks may thus increase the mortality rate for seals.

At FFS, the peak period of adult male inflicted injuries (June–July) did not overlap with the peak period of shark-inflicted injuries (April–May). This may indicate that sharks have less opportunity at FFS than at Laysan Island to attack seals involved in mobbing incidents. Alternatively, large sharks may be present at FFS later in the year, when fewer mating injuries occur, or their attacks upon injured seals at FFS may be rarely documented.

Of the six types of injuries observed on Hawaiian monk seals, those with the most potential to affect the population are caused by adult male monk seals during mating attempts and by large sharks. Adult male inflicted mating injuries were seen more often than other types of injuries and were inflicted mostly on females; shark-inflicted injuries may increase the mortality rate for such injured females. These two types of injuries are significant to the extent that they could negatively affect female survival and productivity, both of which are critical to population growth (Eberhardt 1985) of this endangered species.

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# Significance of wounding to female reproductive success in Hawaiian monk seals (*Monachus schauinslandi*) at Laysan Island

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We studied reproductive rate, length of lactation period, pup survival, and mortality of injured and uninjured female Hawaiian monk seals (*Monachus schauinslandi*) on Laysan Island, northwestern Hawaiian Islands, in 1983–1989. The severity and timing of nonfatal injuries were influential in determining their effect on female reproductive success. There was a tendency towards a shorter mean lactation period and lower survival rate of pups for females with major injuries than for uninjured females. Females with minor injuries were similar to uninjured females in terms of reproductive rate, length of lactation, and pup survival. For females injured shortly before the birth of their pup or during lactation, pup survival was lower than for uninjured females, whereas for females injured during the year prior to pupping, measures of reproductive success were not significantly different from those for uninjured females. Immature (aged 4–8 years) females entering the reproductive population were injured by adult male seals significantly more often than females aged 0–3 years, but at a similar rate to adult females. The major effect of injuries on female reproductive success is an increase in female mortality: 87.5% of the adult females ($n = 16$) that died on Laysan Island in 1983–1989 sustained injuries from adult male seals.

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Nous avons étudié le taux de reproduction, la durée de l'allaitement, la survie des petits et la mortalité des femelles blessées et saines dans une population de Phoques-moines (*Monachus schauinslandi*) sur l'île Laysan dans le nord-ouest de l'Archipel hawaïen de 1983 à 1989. L'effet des blessures non mortelles sur le succès de la reproduction des femelles dépendait de l'importance de la blessure et de la période où elle se produisait. Les femelles portant des blessures graves avaient tendance à allaiter moins longtemps en moyenne que les femelles saines et leurs petits avaient un taux de survie moindre. Les femelles n'ayant que des blessures superficielles avaient un taux de reproduction, une période d'allaitement et un taux de survie de leurs petits qui ne différaient pas de ceux des femelles saines. Les femelles blessées peu avant la mise bas ou durant la période d'allaitement avaient plus tendance à perdre leurs petits que les femelles saines; toutefois, une blessure reçue un an avant la mise bas n'affectait pas de façon significative le taux de reproduction. Les femelles immatures, âgées de 4–8 ans, qui commençaient leur vie reproductive, recevaient plus de blessures de la part des mâles adultes que les femelles âgées seulement de 0–3 ans, mais tout autant que les femelles adultes. L'effet principal des blessures sur la reproduction est lié à la mortalité des femelles : 87,5% des femelles adultes mortes sur l'île Laysan en 1983–1989 ($n = 16$) portaient des blessures causées par des mâles adultes.

[Traduit par la rédaction]

## Introduction

In recent years, efforts to identify factors contributing to a decrease in the survival and productivity of Hawaiian monk seals (*Monachus schauinslandi*) have increased as part of an overall recovery plan (Gilmartin 1983, 1988). Counts of monk seals have declined from about 1000 in 1959 to approximately 580 in 1987 (Johnson *et al.* 1982; Gilmartin 1988). In this situation, even a slight decrease in female survival or productivity could have a significant negative impact on population dynamics, as the net growth of a pinniped population is dependent on, and most sensitive to, female survival and, to a lesser extent, female reproductive success (Eberhardt and Siniff 1977; Eberhardt 1985). Wounds inflicted on adult females by males during mating attempts are the most common type of injury observed in monk seals (Hiruki *et al.* 1993). Consequently, the occurrence of such injuries and their potential effect on reproductive success have become matters of concern (Gilmartin 1983).

Female reproductive success (i.e., the number of viable offspring produced by a female during her lifetime) can be subdivided into several components, such as survival of the female to breeding age, reproductive life-span, and the production and survival of offspring (Clutton-Brock 1988), all of which

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could be influenced by injuries. In long-lived animals such as monk seals that can reproduce until at least 25 years of age (Johanos *et al.* 1990), longevity is a significant component of the lifetime reproductive success of females (Le Boeuf and Reiter 1988; Thomas and Coulson 1988), particularly if only one offspring is produced per year. If injuries increase the mortality of female monk seals, their lifetime productivity will be reduced.

Injuries to adult female monk seals could affect the production of pups in several ways. A wounded female may be less likely to breed because her resources are needed to ensure her own survival, or if she does breed, her pup may be aborted. Injured female northern elephant seals (*Mirounga angustirostris*) did not copulate in the year that they were injured and thus did not pup in the year following the injury (Le Boeuf *et al.* 1982).

The survival of pups born to wounded females may also be reduced. If an injured female has a pup, the amount of energy she is able to invest during the nursing period may be less than that of an uninjured female. Energy stored for lactation or for development of her pup might be redirected towards recovery from the injury (Ainley *et al.* 1981). Similarly, a pregnant female recovering from an injury might not be in as good condition at parturition as an uninjured female. Female Hawaiian monk seals fast during the entire nursing period (Kenyon and Rice 1959), as do most other phocid seals (e.g., northern elephant seals (Riedman and Ortiz 1979); harp seals, *Phoca groenlandica* (Lavigne *et al.* 1982); grey seals, *Halichoerus grypus* (Anderson and Fedak 1987)). If a female monk seal is in poor condition when her pup is born, she may be more likely to have a smaller pup or to wean her pup prematurely, because she is not feeding and cannot replenish her energy stores during lactation. A low weight at weaning may reduce the pup's probability of survival through its first year of life.

This paper examines the influence of injuries on four components of female reproductive success (reproductive rate, maternal investment, survival of pups, and mortality of adult females) to test the hypothesis that injuries inflicted by adult males negatively affect survival and reproduction. We also evaluate the significance of injury to the recruitment of young females into the breeding population.

## Methods

The reproductive histories and injuries of female Hawaiian monk seals were analyzed from data collected at Laysan Island, a low coral and sand island located northwest of the main Hawaiian Islands (latitude 25°42′N, longitude 171°44′W), during 24 April – 21 July 1983, 30 March – 6 August 1984, 6 March – 1 December 1985, 1 May – 4 August 1986, 6 April – 22 July 1987, 28 February – 21 June 1988, and 30 March – 14 July 1989. Females were identified by temporary marks applied with commercial bleach at the beginning of the field season, by natural markings or scars, or by flipper tags applied in previous years (e.g., Stone 1984; Hiruki *et al.* 1993). For each female with a pup, the date of parturition, weaning date, and the pup's permanent identification number were also recorded. Pups were tagged after they had been weaned (Johanos *et al.* 1987; Johanos and Austin 1988; Alcorn and Buelna 1989; Johanos *et al.* 1990). Data recorded for each injured female included identification number, size class, location of the seal, and description of the injury, as detailed in Hiruki *et al.* (1993).

Female monk seals were classified as adult or immature on the basis of estimated age. Because reproductive success might be affected by age rather than injury status, seals that matured during the study period were excluded from the analysis of reproductive success. Adults were seals classed as being of breeding size in 1983, according to their length, girth, pelage appearance, and scarring (Stone 1984), or seals that had a pup in 1983 or earlier. Immatures were seals seen as juveniles or subadults in 1983 or 1984, or seals that were born in 1983 or later.

To evaluate the impact of injuries on reproductive success, adult female monk seals were divided into three categories in each year: *uninjured*: females that did not sustain any injuries prior to parturition or in the previous year; *currently injured*: females injured during the current year, before parturition or while still nursing the pup; and *previously injured*: females injured in the previous year, usually after weaning the pup of that year. The last category also included females that were injured in the previous year and were not observed with a pup.

Injuries were classified as minor or major. Minor wounds were circular wounds inflicted by cookiecutter sharks (*Isistius brasiliensis*), wounds inflicted by seals in jousting incidents, or those inflicted by the seal contacting a coral reef or debris (Hiruki *et al.* 1993). Major wounds were dorsal lacerations or gaping wounds inflicted by adult male seals during mating incidents or injuries caused by large sharks (described in Hiruki *et al.* 1993). Some of the wounds inflicted by adult males did not appear to be severe externally (e.g., Fig. 2A, 2B, Hiruki *et al.* 1993), but were classified as major because superficially minor abrasions and lacerations may mask significant subcutaneous damage (Johanos and Austin 1988), and some females die after sustaining seemingly minor wounds from adult male monk seals (Johanos *et al.* 1990; T. C. Johanos, B. L. Becker, and L. M. Hiruki, personal observations).

The reproductive rate, defined as the proportion of females that have a pup in a particular year, of uninjured females was compared with that of females injured in the previous year. The currently injured females were excluded from the analysis of reproductive rate because, by definition, they all had pups.

The parental investment period (the number of days that a female nurses and defends her pup) was calculated from the birth and weaning dates of each pup. If a range of dates was recorded for birth or weaning (e.g., 1–3 March), the last day in the range (3 March) was used to calculate the parental investment period. The lengths of completed parental investment periods of currently and previously injured females were compared, as were those of injured and uninjured females. If a female's parental investment period was cut short because her pup died or because she lost her pup to another female and did not gain another (Johnson and Johnson 1978; Boness 1990), it was excluded from the analysis, so that only complete nursing periods were considered. Females with major and minor injuries were compared independently with uninjured females to assess the effect of severity of injury on parental investment.

Pup survivorship was measured in two ways: the proportion of pups alive at the end of the nursing period and the proportion of pups alive after their first year. The survivorship of the pups of currently injured females and those of previously injured females was compared, and each was compared independently with pups of uninjured females. Pups of females with major and minor injuries were compared independently with pups of uninjured females.

The reproductive histories of all permanently identified adult female seals were examined in relation to the number of major injuries sustained per year in 1988 and 1989. The distribution of major injuries within years (number of injuries per year for each seal) was compared with a Poisson distribution to determine whether some females received a disproportionate fraction of the injuries. The number of identified female seals that died or disappeared from Laysan Island during 1983–1989 was examined to determine how many were known to have been injured by adult males.

Immature seals were divided into two classes, based on their reproductive maturity and age in 1988 and 1989. Seals aged 0–3 years were classed as prereproductive. This classification is based on 5 years being the youngest observed age of first reproduction for Hawaiian monk seals (Johanos *et al.* 1990); hence, the minimum age of first estrus appears to be 4 years, since female monk seals mate

TABLE 1. Power of tests used to compare components of reproductive success between injured and uninjured female Hawaiian monk seals at Laysan Island, northwestern Hawaiian Islands, 1983–1989, and the sample size required to determine a significant difference between the observed proportions when the power of the test = 0.80 ($\alpha$ = 0.05; one-tailed test)

| Comparison | Test statistic | Power of test | Sample size required |
|---|---|---|---|
| Reproductive rate | | | |
| Major vs. uninjured | $G = 0.599$ | 0.19 | 783 |
| Minor vs. uninjured | $G = 0.024$ | 0.10 | 5601 |
| Parental investment | | | |
| Major vs. uninjured | $t = 0.981$ | 0.31 | 49 |
| Minor vs. uninjured | $t = 0.723$ | 0.17 | 260 |
| Survival to weaning | | | |
| Injured vs. uninjured | $G = 5.53$ | 0.82 | 137 |
| Survival through first year | | | |
| Major | | | |
| Current vs. uninjured | $G = 2.92$ | 0.30 | 44 |
| Previous vs. uninjured | $G = 0.002$ | 0.07 | 2953 |
| Pooled vs. uninjured | $G = 1.01$ | 0.1 | 1043 |
| Minor | | | |
| Pooled vs. uninjured | $G = 2.56$ | 0.40 | 138 |

the year before they give birth. Seals aged 4–8 years were classed as transitional, because they were starting to enter the reproductive cohort.

To determine the age-class of immature females injured most frequently by adult males, the proportions in the prereproductive (aged 0–3 years) and transitional (aged 4–8 years) classes of immature seals injured by adult males in 1988 and 1989 were compared.

For comparing two proportions, a 2 × 2 $G$-test with the Williams correction was used (Sokal and Rohlf 1981). Because of the small size of the samples tested, the power of the tests comparing injured and uninjured females was calculated. Also calculated was the sample size needed to be 80% certain of detecting a significant difference between two samples (Casagrande *et al.* 1978; Sokal and Rohlf 1981).

## Results

Data were available on 55 individually identified adult female seals and 10 untagged and 99 tagged immature female seals. Thirteen adult and 2 untagged immature female seals were identified in all years from 1983 through 1989. Only partial records were available for the remaining 42 adult and 8 untagged immature females. All tagged animals were easily identifiable between years; seals identified only by means of minor scars or marks applied with bleach were not consistently identified between years.

### *Power of tests*

The power of most tests used to examine the differences between injured and uninjured females was low (Table 1). Given the proportions compared, the sample sizes required to detect a significant difference between injured and uninjured females were substantial.

### *Reproductive rate and pup survivorship*

No effect due to severity of injury on the reproductive rate of females injured in the previous year was detected (Table 2). The reproductive rates of females with major injuries ($n = 25$; $G = 0.599$, df = 1, $p = 0.474$) and those with minor injuries ($n = 7$; $G = 0.024$, df = 1, $p = 0.892$) were similar to that of uninjured females ($n = 201$).

Of the six pups that died prior to weaning, two had uninjured mothers, two had mothers with a major injury, and two had mothers with a minor injury. No significant difference was detected in survivorship to weaning of pups of females with major injuries, currently ($n = 7$) and previously ($n = 13$; $G = 0.25$, df = 1, $p = 0.687$). Survival to weaning was similar for pups of females with major injuries ($n = 18/20$) and those with minor injuries ($n = 9/11$; $G = 0.361$, df = 1, $p = 0.585$). When the major and minor injury classes were pooled, pup survival to weaning ($n = 27/31$) was significantly lower than that of pups of uninjured females ($n = 119/121$; $G = 5.53$, df = 1, $p = 0.027$).

Survival through the first year of life did not differ significantly for pups of females with major injuries currently ($n = 7$) and previously ($n = 13$; $G = 1.98$, df = 1, $p = 0.229$, Table 2). Pups of currently injured females had slightly lower survival than pups of uninjured females ($n = 121$; $G = 2.92$, df = 1, $p = 0.091$), though the difference was not statistically significant. Pups of females previously with major injuries had survivorship similar to pups of uninjured females ($G = 0.002$, df = 1, $p = 0.965$). Survivorship of pups of injured females (currently and previously injured classes pooled) did not differ significantly from that of pups of uninjured females ($G = 1.01$, df = 1, $p = 0.401$).

Survival through the first year was similar for pups of currently ($n = 7$) and previously ($n = 4$) injured females with minor injuries ($G = 0.045$, df = 1, $p = 0.874$). No difference was detected between the survivorship of pups of females with minor injuries (currently and previously injured classes pooled) and uninjured females ($G = 2.56$, df = 1, $p = 0.126$).

### *Parental investment*

Females with major injuries did not appear to invest significantly less in their pups than did uninjured females. The parental investment period of previously injured females with major injuries ($n = 6$, $\bar{x} = 38.8 \pm 5.6$ d) was similar to that of uninjured females ($n = 74$, $\bar{x} = 41.1 \pm 3.8$ d; Mann–Whitney normal approximation, $t = 0.918$, $p = 0.179$). Currently injured females with major injuries ($n = 2$) invested the same amount of time in their pups ($\bar{x} = 40 \pm 1.0$ d) as previously injured females (Mann–Whitney $U$-test: $U = 6.5$, $p > 0.5$). When both currently and previously injured classes were combined, females with major injuries ($n = 8$) invested a similar amount of time in their pups ($\bar{x} = 39.13 \pm 4.8$ d) to uninjured females (Mann–Whitney normal approximation: $t = 0.981$, $p = 0.163$).

The parental investment period of currently injured females with minor injuries ($n = 6$, $\bar{x} = 41.8 \pm 4.2$ d) did not differ significantly from that of previously injured females ($n = 2$, $\bar{x} = 41.5 \pm 3.5$ d; Mann–Whitney $U$-test: $U = 11$, $p > 0.05$). Injured females (currently and previously injured classes combined, $n = 8$, $\bar{x} = 41.75 \pm 3.8$ d) and uninjured females had similar investment in their pups (Mann–Whitney normal approximation: $t = 0.723$, $p = 0.235$).

### *Frequency of injury and mortality of females*

Thirty-seven of 55 adult female seals (67%) did not sustain a major injury in 1988 or 1989 (Table 3). The distribution of the number of major injuries per year for adult female seals did not differ significantly from a Poisson distribution ($G = 1.87$, df = 1, $p > 0.1$).

Eight of 55 permanently identified adult female monk seals

TABLE 2. Survivorship through the first year of life of pups of injured and uninjured female Hawaiian monk seals, Laysan Island, northwestern Hawaiian Islands, 1983–1989

| | Females with major injuries | | Females with minor injuries | | Uninjured females |
|---|---|---|---|---|---|
| | Current[a] | Previous[b] | Current[a] | Previous[b] | |
| No. of pups that survived | 2 (29) | 9 (69) | 3 (43) | 2 (50) | 79 (65) |
| No. of pups that did not survive | 4 (57) | 4 (31) | 4 (57) | 2 (50) | 33 (27) |
| No. of pups with fate unknown | 1 (14) | 0 (0) | 0 (0) | 0 (0) | 9 (8) |
| Total no. of pups | 7 | 13 | 7 | 4 | 121 |
| Total no. of females | 7 | 25 | 7 | 7 | 201 |
| % of females with pup | 100 | 52 | 100 | 57 | 60 |

NOTE: Numbers in parentheses are percentages.

[a] Seals injured before or during parental investment.

[b] Seals injured in the previous year after the end of parental investment, or during a year in which they were not seen with a pup.

TABLE 3. Number of major injuries per year for adult female Hawaiian monk seals at Laysan Island, northwestern Hawaiian Islands, 1988 and 1989

| No. of injuries per year | Number of female monk seals | | | Expected frequency |
|---|---|---|---|---|
| | 1988 | 1989 | Pooled | |
| 0 | 25 | 12 | 37 | 34.28 |
| 1 | 5 | 7 | 12 | 16.21 |
| 2 | 1 | 3 | 4 | 4.43 |
| 3 | 2 | 0 | 2 | |
| Total | 33 | 22 | 55 | |

NOTE: Expected frequencies are generated from a Poisson distribution.

TABLE 4. Numbers of immature female Hawaiian monk seals injured in the transitional (T; aged 4–8 years) and prereproductive (P; aged 0–3 years) classes at Laysan Island, northwestern Hawaiian Islands, 1988 and 1989

| | 1988 | | 1989 | | Pooled | |
|---|---|---|---|---|---|---|
| | P | T | P | T | P | T |
| No. of females injured | 4 | 4 | 3 | 12* | 7 | 16* |
| Total no. of injuries | 4 | 7* | 3 | 15* | 7 | 22* |
| No. of females not injured | 46 | 23 | 41 | 20 | 87 | 43 |
| Total no. of females | 50 | 27 | 44 | 32 | 94 | 59 |

*Significant difference between transitional and prereproductive classes.

died in 1983–1989. All eight had sustained injuries inflicted by adult male monk seals shortly before their death. Two unidentified adult females died of unknown causes, perhaps age-related, in 1983; however, one had two small punctures on her back and the other carcass was being mounted by an adult male seal. Six unidentified females died in 1983–1989; all had sustained injuries inflicted by adult male monk seals. Of the uninjured females, three (two in 1983, one in 1988) that were easily identified by natural marks were not seen in any subsequent years. Thus, 14 of 16 adult females that died had been injured by adult males shortly before their death.

One untagged immature female and 4 of 26 females aged 3–6 years died after sustaining injuries from adult male seals. Two immature females identified from flipper tags disappeared after sustaining adult male inflicted injuries, and were not seen in subsequent years.

### *Effect of injuries on recruitment of immature females*

In 1988, no significant difference was detected in the proportion of transitional immature female seals aged 4–8 years ($n = 4/27$) and prereproductive females aged 0–3 years ($n = 4/50$; $G = 0.78$, df = 1, $p = 0.442$; Table 4) that were injured by males. Although the difference between the two classes was not statistically significant, wounding of transitional females (15% of the class) was almost double that of prereproductive females (8% of the class), which is consistent with the results from 1989, when a greater proportion of transitional than prereproductive immatures was injured ($n = 12/32$ and $3/44$, respectively; $G = 10.86$, df = 1, $p < 0.001$). Moreover, many females in the transitional class, but none in the prereproductive class, were injured more than once (Table 4). The number of injuries per female was significantly greater for the transitional class than for the prereproductive class in both years (1988: $G = 4.16$, df = 1, $p = 0.043$; 1989: $G = 16.56$, df = 1, $p < 0.001$). The proportion of immature females in the transitional class that were injured by adult males in 1988 and 1989 ($n = 16/59$; Table 4) was similar to that of adult females ($n = 18/55$; Table 3; $G = 0.42$, df = 1, $p = 0.494$).

## Discussion

We cannot conclude that injuries have no effect on reproductive success, though the hypothesis that injuries negatively affect female reproductive success was only weakly supported. Because the sample sizes were small, the power of the tests used to compare injured and uninjured females was low (Table 1), and the probability of committing a type II error was high. The power of a test can be improved by increasing the sample size (Sokal and Rohlf 1981); however, the sample sizes required to find significant differences between injured and uninjured females in our study were in most cases very large (Table 1). The probability of observing injuries with such high frequency in a small population of adult females (55 permanently identified seals) was very low. Despite the low power of the tests, pup survival showed some negative effects due to injury. Pups of females with major injuries appeared to survive less well than those of uninjured females. Pups of injured females (all classes pooled) had significantly lower survivorship to weaning than pups of uninjured females, and pups of currently injured females with major wounds had slightly lower survival through the first year than pups of uninjured females (Table 2). Thus, despite small sample sizes, there is some evidence that injuries affect female reproductive success.

The timing of an injury to a female could influence the amount of energy she has during lactation, which in turn could affect the pup's survival through its first year. Lactation is energetically costly for females (Young 1976). Because female phocids generally do not feed during lactation, they use a significant proportion of their energy reserves to feed their pups. For example, female grey seals use 85% of their stored energy resources while nursing their offspring (Fedak and Anderson 1982), northern elephant seals use 58% (Costa *et al.* 1986), and hooded seals (*Cystophora cristata*) use 33% (Bowen *et al.* 1987). A female in poor condition because of a recent injury may have a lower than normal supply of stored fat available for lactation, resulting in reduced pup survival.

Although the survival of pups of currently injured females was not significantly different than for pups of uninjured females (Table 2), there is some evidence that currently injured females use energy, otherwise allocated for lactation, to recover from injuries. Two female monk seals that sustained severe injuries inflicted by sharks shortly prior to pupping at French Frigate Shoals (latitude 23°45′N, longitude 166°10′W) in the northwestern Hawaiian Islands could not nurse their pups and eventually abandoned them (M. P. Craig, Honolulu Laboratory, personal communication). One female injured by adult male seals at Kure Atoll (latitude 28°25′N, longitude 178°10′W) also abandoned her pup within days of its birth (J. R. Henderson, Honolulu Laboratory, personal communication).

Poor condition of females before parturition may reduce the survival of their offspring. Female northern elephant seals arriving for the breeding season with fresh shark wounds were less successful at pupping and breeding than uninjured females (Ainley *et al.* 1981; Le Boeuf *et al.* 1982). The pups of injured female elephant seals were stillborn or abandoned soon after birth, or wounded mothers allowed other females to nurse their pups. The injuries sustained by elephant seals affected their ability to successfully wean their pups. Ainley *et al.* (1981) found that females that had raised pups successfully to weaning age in the years prior to their injury were less successful in raising their pup during the year in which they were injured. Thus, wounds that result in the condition of females being poorer than normal apparently cause reduced survival of offspring to weaning.

After weaning, a pup fasts for a number of weeks and may therefore need a minimum amount of energy from the nursing period to survive. The postweaning period is critical because the pup is relatively defenseless and inexperienced, and must live on stored energy until it learns to feed on its own (Reiter *et al.* 1978). Hawaiian monk seal pups lose approximately 15–30% of their weaning weight in the postweaning fast (Kenyon and Rice 1959), and most of the energy used during this period appears to be from blubber accumulated during nursing. About 94% of the energy required by grey seal pups during the first month of their postweaning fast comes from blubber stored during the nursing period (Nordoy and Blix 1985; Worthy and Lavigne 1987). Similarly, harp seal pups obtain 80–90% of their energy from blubber acquired in the nursing period (Worthy and Lavigne 1983, 1987). Because of the high energetic cost of the postweaning fast, a pup weaned at a lighter than normal weight would probably be less likely to survive its first year. Consequently, the first-year survival of pups of currently injured females may be detrimentally affected by their mothers' wounds (Table 2).

In contrast to currently injured females, females injured in the year prior to parturition appear to have recovered sufficiently to store normal energy reserves. Reproductive rate, mean parental investment period, and pup survivorship of previously injured females were not significantly different from those of uninjured seals. Most pregnant grey seals do not start increasing in weight until the time of implantation of the blastocyst (approximately 3–4 months after copulation; Boyd 1984). Johnson and Johnson (1978) found that many Hawaiian monk seal females had regained most of the weight lost during lactation after 42–66 days, before undergoing an extended (20–30 d) stay on shore to moult. Monk seals appear to fast or to eat very little during the moult (Kenyon and Rice 1959). If female Hawaiian monk seals do not begin storing energy for lactation until after they moult, a previously injured female would have several months to recover from her wound before starting to deposit fat reserves for lactation, and her pup would be more likely to receive the full nutritional benefit of lactation than the pup of a currently injured mother.

A wounded female monk seal's reproductive success appears to be influenced by the severity of her injuries. Minor injuries had no detectable effect on the reproductive success of female monk seals. Reproductive rate, mean parental investment period, and survivorship of the pups of currently and previously injured females with minor wounds were the same as for uninjured females. Major injuries negatively affected the reproductive success of currently injured females with respect to pup survivorship (Table 2). Le Boeuf *et al.* (1982) monitored 11 female northern elephant seals with "moderate to severe" fresh wounds and suggested that the injured females successful in raising their pups appeared to have the least severe injuries.

Most of the female seals that died at Laysan Island sustained injuries inflicted by adult males before they died. Some of the females that died did not appear to have injuries that were serious enough to be fatal (Hiruki *et al.* 1993). In these cases, it may have been the continued harassment of the males during a mobbing incident, where several males attempt to mate with a female, that resulted in wounding sufficient to cause death. Some female seals are reinjured often enough in the same year by adult males (Table 3) that the cumulative effect may result in the death of the female. Similarly, female northern elephant seals sometimes die after being harassed by groups of subordinate males (Le Boeuf and Mesnick 1990). A female elephant seal departing from the harem may be chased by several subordinate males, all of which attempt to mount her. During this time, she receives over 20 times more blows, mounts, and copulations than normal, and if she dies, males sometimes compete over her carcass (Le Boeuf and Mesnick 1990). Female mink (*Mustela vison*) have also been known to die after being pursued by, and mating with, several males (Hatler 1972). The female sustains neck injuries during mating, but generally these are not severe enough to be fatal (Hatler 1972). Hatler (1972) has suggested that because the males pursue her frequently, she probably cannot hunt and replenish her energy reserves and dies as a result of the continued harassment.

Immature female Hawaiian monk seals were injured more often by adult males as they entered the reproductive population than when they were prereproductive (Table 4). The proportion of immature females aged 4–8 years with injuries was similar to that of adult females. Immature females sometimes die from these injuries: 4 of 26 females aged 3–6 years in 1988 and 1989 sustained fatal injuries. Mortality of young females is a serious concern with respect to population growth, as their potential productivity is never realized, thus reducing future recruitment into the population.

In summary, the major consequence of injuries for female reproductive success is the increase in female mortality, which shortens their reproductive life. The timing and severity of injuries can affect the survivorship of pups of injured females if the females do not have sufficient time to recover before parturition and lactation. However, if the females have sufficient time between sustaining injuries and parturition, there appears to be no major effect on the survival of pups to weaning and through the first year of life.

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# Horizontal and Vertical Movements of the Shortfin Mako Shark, *Isurus oxyrinchus*, in the Southern California Bight

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*Abstract*

Recreational and commercial fishing effort directed at the shortfin mako shark, *Isurus oxyrinchus*, off the coast of southern California increased markedly in the mid 1980s. However, very little is known about the population size, stock structure or movements of these sharks in the northern Pacific. It is important to determine their role in these waters because the southern California bight may be an important pupping and nursery area for shortfin mako sharks.

Acoustic telemetry was used to identify short-term horizontal and vertical movements of three shortfin mako sharks in the southern California bight during the summer of 1989. All three sharks were two-year-old juveniles and were tracked for periods of from 18 to 25 h. They spent 90% of their time in the mixed layer, with only infrequent excursions below the thermocline. Vertical and horizontal movements did not indicate any diel activity pattern associated with distance to the shore or nearby islands or with bottom topography.

*Extra keywords:* tagging, tracking, water temperature.

## Introduction

Recreational and commercial fishing effort directed at the shortfin mako shark, *Isurus oxyrinchus*, off the coast of southern California increased markedly during the 1980s (Holts 1988). Popular interest in the shortfin mako shark as a sportfish and consumer acceptance of it as a commercial foodfish encouraged continued harvests. Popularity with sportfishers on both chartered sportfishing vessels and private boats has increased by an order of magnitude in recent years. Estimated fishing effort in angler trips (number of individual angler fishing trips) increased from 41 000 in 1986 to more than 410 000 in 1989 and may still be increasing (S. Crook, California Dept. of Fish and Game, personal communication). Approximately 90 to 180 t (metric tonnes dressed weight) of shortfin mako sharks are taken commercially as an incidental catch in the Californian drift-net fisheries for thresher sharks, *Alopias vulpinus*, and swordfish, *Xiphias gladius* (Bedford and Hagerman 1983; Holts 1988; Hanan *et al.* 1993). An experimental longline fishery targeting shortfin mako sharks began off southern California in 1988 and continued through the 1991 fishing season. An additional 68 t of shortfin mako sharks were landed annually in this fishery. Total commercial landings of shortfin mako sharks for all southern Californian coastal fisheries exceeds 200 t annually. This has raised concerns about the ability of the resource to sustain the current level of fishing pressure. Very little is known about the population size, stock structure, distribution or movements of the shortfin mako shark off the US Pacific coastal states. Catch records from the California Department of Fish and Game indicate that the fisheries take shortfin mako sharks primarily within 93 km of shore and from the California–Mexico border to as far north as San Francisco. They are available in greatest abundance in the spring and summer months; catches are greatest between June and August.

0067-1940/93/060901$05.00

The catch is composed almost entirely of juvenile 1- and 2-year-old fish weighing from 13·6 to 27·2 kg (Hanan *et al.* 1993). The southern California bight may serve as a nursery area for newborn and juvenile shortfin mako sharks (Holts and Bedford 1989).

Shortfin mako sharks grow slowly, mature relatively late in life, and have a long gestation period (Pratt and Casey 1983). They produce a few (generally 4 to 16) well developed pups (Stevens 1983) whose survival is assumed to be good because of their advanced development at birth. This life-history strategy makes these sharks quite vulnerable to modern commercial and recreational fishing operations.

Information on distribution and short- and long-term movement patterns is necessary in assessing the status of affected stocks and in determining management options should management of coastal shark fisheries become prudent. Conventional dart-tagging studies in the north-western Atlantic have yielded considerable information concerning long-term movements of shortfin mako sharks in that area (Casey and Kohler 1992), but studies conducted off the southern Californian coast have only begun to reveal long-term movements of shortfin mako sharks there. Still less is known about the short-term behaviour of individuals. Acoustic telemetry has proved to be useful in identifying the short-term horizontal and vertical movements of several shark species (Carey 1990; Carey and Scharold 1990; Nelson 1990) and other large pelagic fish species (Carey and Robison 1981; Holland *et al.* 1990*a*, 1990*b*; Holts and Bedford 1990; Brill *et al.* 1993).

During the summer of 1989, four five-day cruises were conducted through a cooperative agreement between the Southwest Fisheries Science Center and the California Department of Fish and Game. The primary objective was to determine short-term movements and activity patterns of shortfin mako sharks in the waters off southern California by using acoustic telemetry.

## Materials and Methods

The 18-m sportfishing vessel *Pacific Clipper* was chartered from 14 August to 15 September 1989. The acoustic tracking techniques and equipment used in this study were identical to those previously described for tracking striped marlin (Holts and Bedford 1990). This involved the use of a hull-mounted directional hydrophone and ultrasonic receiver (Vemco[1] CS40 and VR60, respectively) to indicate direction and approximate distance to the tagged shark. The acoustic transmitter tags (Vemco[1] V4P) had working pressures of 100 psi and 500 psi (working depths of 0 to 70 m and 0 to 340 m, respectively). The tracking vessel remained within 400 m of the fish, and loran-C coordinates were recorded every 15 min for horizontal positioning. Temperature profiles of the water column were measured with expendable bathythermographs approximately every 6 h.

Sharks were captured by rod and reel. Terminal tackle consisted of a 5-m length of leader constructed from braided wire (250-pound test) and a size '9/0' hook baited with Pacific mackerel, *Scomber japonicus*, or Pacific sardine, *Sardinops sagax*. Sharks were attracted to the vessel by chumming with finely chopped mackerel. Of 28 shortfin mako sharks captured, only the three largest were selected for tagging with acoustic transmitters. To minimize capture trauma, these sharks were quickly brought alongside the boat, where the transmitters were attached with a hand-held harpoon applicator without removing the sharks from the water. They were then released by cutting the leader as close to the hook as possible. Tracking commenced immediately after each fish was released. Total length and weight were estimated while the fish was being tagged.

## Results

All three sharks were tagged and tracked off Oceanside, California, in the channel formed by Santa Catalina and San Clemente Islands (Fig. 1). Tracking periods ranged from

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

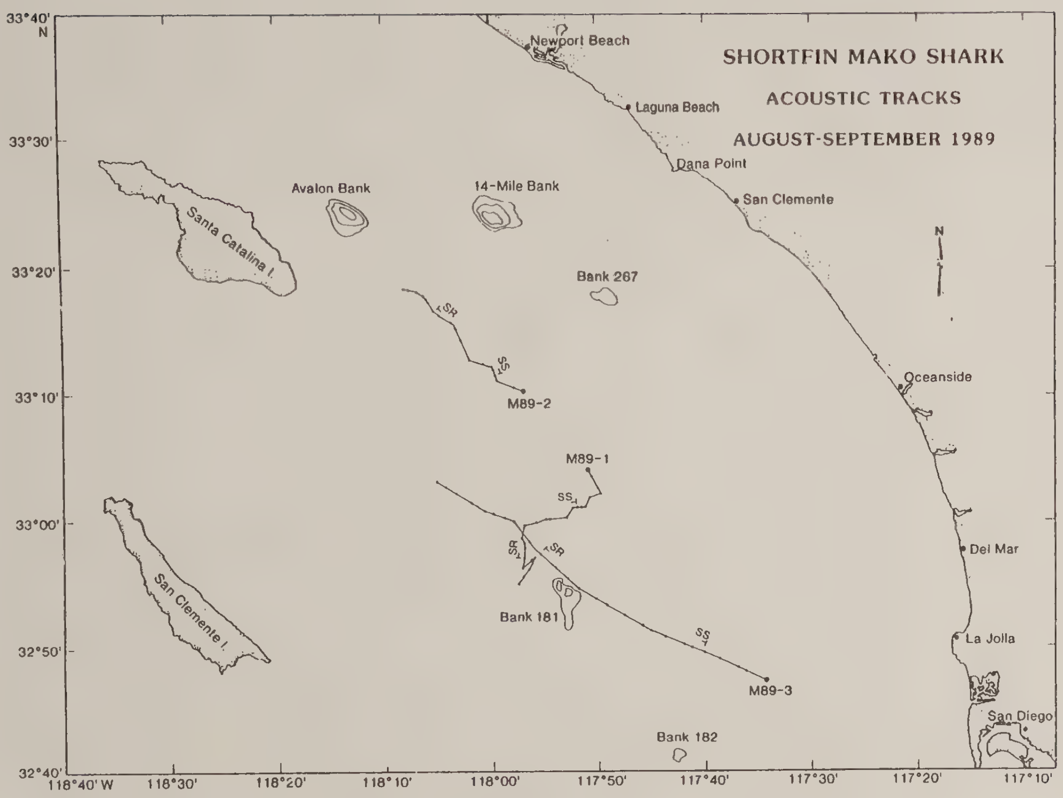
SHORTFIN MAKO SHARK
ACOUSTIC TRACKS
AUGUST-SEPTEMBER 1989
N
Newport Beach
Laguna Beach
Dana Point
San Clemente
Oceanside
Del Mar
La Jolla
San Diego
Santa Catalina I.
San Clemente I.
Avalon Bank
14-Mile Bank
Bank 267
Bank 181
Bank 182
M89-1
M89-2
M89-3
SR
SS
33°40' N
33°30'
33°20'
33°10'
33°00'
32°50'
32°40'
118°40' W
118°30'
118°20'
118°10'
118°00'
117°50'
117°40'
117°30'
117°20'
117°10'

**Fig. 1.** Horizontal movements of three shortfin mako sharks acoustically tracked in the southern California bight, August–September 1989. SR, sunrise; SS, sunset.

18 to 25 h and covered 24 to 57 km. Data for both horizontal movements and vertical depth variations were obtained for all tracks. The location of the shark was assumed to be the same as that of the tracking vessel. Loran-C positions recorded every 15 min were smoothed with a running average over 90-min periods to indicate rate of movement.

The first shortfin mako shark tracked (Shark M89-1) was estimated to be a 1·8-m, 36-kg female and was tagged at 1300 hours on 15 August 1989. It was released 18 km north of the '181 Fathom Bank' (at 33°06′N,117°52′W), and it moved 30 km in a generally southerly direction over the next 25 h (Fig. 1). The overall rate of movement was 1·10 km $h^{-1}$ (Fig. 2). Speed decreased from about 2·0 km $h^{-1}$ after release to less than 0·74 km $h^{-1}$ just before sunset, then increased markedly to 2·78 km $h^{-1}$ at 2030 hours. Speed gradually declined during the remainder of the night to 0·74 km $h^{-1}$ just after sunrise. Between sunrise and the end of the track, this fish again increased its speed to about 1·80 km $h^{-1}$.

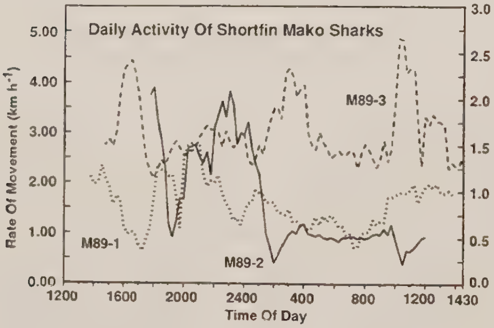

**Fig. 2.** Daily activity, in kilometres per hour and nautical miles per hour, for three shortfin mako sharks tracked in the southern California bight, August–September 1989.

This shark initially sounded to 35 m but slowly ascended over the next 45 min to about 7 m, where it remained until 1630 hours (Fig. 3). Between 1630 and 2000 hours, it made

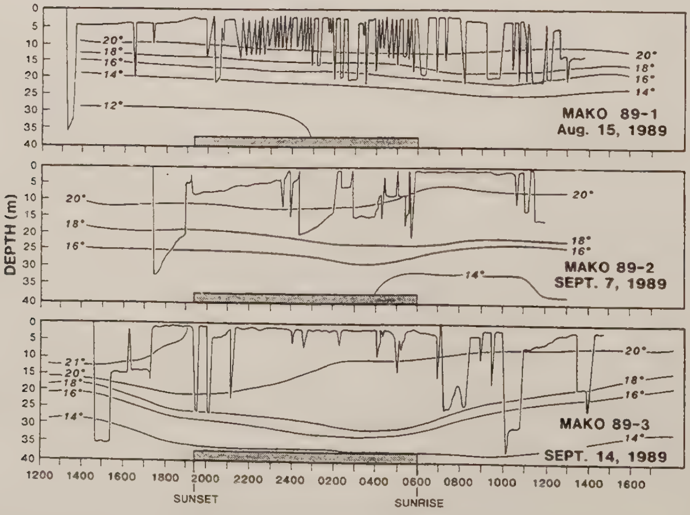

**Fig. 3.** Diving profiles for three shortfin mako sharks in the southern California bight, August–September 1989. Temperatures shown in °C.

two short-duration dives, returning each time to a depth of 4 to 5 m. Sunset occurred at 1930 hours, and the shark began making numerous, almost rhythmic, dives between 3 and 20 m. This pattern continued until sunrise and totalled 32 dives, or an average of 3·5 dives $h^{-1}$. The deepest and longest of these was to 21 m for 23 min at 0300 hours. Dive frequency decreased to less than 2 dives $h^{-1}$ soon after sunrise. This shark spent little time below the steepest gradient of the thermocline.

The second shark tracked (Shark M89-2) was a 1·7-m individual estimated to weigh 32 kg. Its sex was not determined. Tagging and release occurred 30 km north of the '181 Fathom Bank' (i.e. at 32°54′N,117°53′W) at 1730 hours on 7 September 1989 (Fig. 1). This shark travelled 24 km north-west in 18 h and averaged 1·29 km $h^{-1}$ during the daylight hours and 1·48 km $h^{-1}$ at night. As with Shark M89-1, speed decreased from a post-release high of 3·7 km $h^{-1}$ to less than 0·92 km $h^{-1}$ just after sunset. Speed then increased through midnight but decreased to about 0·92 kn $h^{-1}$ for the remainder of the track (Fig. 2). Prior scheduling required the tracking of Shark M89-2 to be terminated after only 18 h.

After release, this second shark immediately descended to 33 m, where it remained for 90 min before gradually ascending to 20 m (Fig. 2). At 1900 hours, just before sunset, it ascended quickly to about 5 m, where it remained until 2000 hours. It remained above 10 m until about midnight, when it descended to 29 m and slowly rose to 12 m over the next couple of hours. A series of short dives followed until sunrise, when the frequency and depth of dives decreased. Shortly after sunrise, it positioned itself between 2 and 4 m, where it remained for the next 4 h. Another series of short dives commenced at 1030 hours. These dives may have been influenced by our attempts to position the tracking boat in the path of the fish in an unsuccessful effort to recapture this individual. The top of the thermocline varied between 18 and 22 m in depth during this track, but the shark did not descend into it except for the initial plunge.

The third shark tracked (Shark M89-3), a 1·8-m, 32-kg individual, was tagged at 1430 hours on 14 September 1989. Sex was not determined. This fish was tagged 31 km east of the '181 Fathom Bank' (i.e. at 32°47′N,117°34′W), and it moved west-north-west, passing over a shoal area near the '181 Fathom Bank' and covering 57 km during the 24-h tracking period (Fig. 1). This shark differed from the other two by covering nearly twice the distance and averaging 2·40 km $h^{-1}$ (Fig. 2). The speed of this shark increased to more than 4·44 km $h^{-1}$ during the first 3 h of the track, and then decreased to almost 2·0 km $h^{-1}$. Speed then remained at about 2·40 to 2·77 km $h^{-1}$ for most of the remainder of the track, with noticeable increases at 0200 and 1000 hours.

When released, Shark M89-3 also sounded to 33 m. Within 1 h it ascended to 15 m, where it remained until 1715 hours (Fig. 3). It then rose to within 1 m of the surface. Just after sunset, it made three dives to 20–25 m. It remained within 3 m of the surface during the night. After sunrise, it descended to 22 m for about 1 h before rising to near the surface. Its deepest dive to 33 m occurred at 1000 hours. This dive and a final one to 19 m at 1300 hours each lasted about 1 h and were well into the upper portion of the thermocline.

## Discussion

### *Post-tagging Dive and Survival*

All three shortfin mako sharks were released in good condition and showed no apparent harmful effects from being tagged throughout the tracking period. There was no apparent trauma from capture extending beyond the post-tagging dive.

Vertical dive profiles indicate that the trauma of capture and release may last only 30 to 90 min. Horizontal movements of Sharks M89-1 and M89-2 support this observation. The actual speed of these two sharks decreased substantially within 2 h of release. The third shark (M89-3) increased its speed over the first 2 h while it remained at a depth of 30 m, then slowed as it ascended into the mixed layer.

An initial dive into the cooler waters below the thermocline immediately following release has been noted for blue sharks, *Prionace glauca*, by Sciarrotta and Nelson (1977), Tricas (1979) and Nelson (1990) and for billfish by Holland *et al.* (1990*a*) and Holts and Bedford (1990). This may be a response of obligate ram ventilators to overcome an oxygen debt built up during capture, as suggested by Holland *et al.* (1990*a*). This is certainly possible in the present case because shortfin mako sharks are active fish when caught on sportfishing gear and undoubtedly expend considerable energy attempting to escape. Both muscular and visceral temperatures in the shortfin mako shark are maintained well above ambient water temperature through a system of vascular counter-current heat exchangers (Carey *et al.* 1981, 1985). The time spent in these post-tagging dives may also be a behavioural response to regulate internal temperature by dissipating excess heat built up during the catching and tagging process.

### *Horizontal Movements in the Southern California Bight*

The southern California bight has a diverse topography that includes several large islands ranging in distance from 20 to 110 km from the Californian shore. The average water depth is 700 to 1000 m in the immediate tracking area, although numerous submarine escarpments and banks rise to within 100 m of the surface. The southern California bight is also influenced by the California Current and counter-current, which forms many eddies in and around the islands. These currents and resulting eddies probably influenced the movement of the sharks we tracked. Water currents were found to influence the movement of striped marlin off the island of Hawaii (Brill *et al.* 1993). Unfortunately, the measurement of water currents and eddies requires current-profiling systems not available on small tracking vessels.

All three tracks in this study began and ended within a few kilometres of various submarine features within the southern California bight. However, there was no clear indication that any of the sharks tracked were actually associated with these features. Each capture and tagging location was influenced by drift because our 'chumming line' extended over several kilometres at times.

Shark M89-1, although moving generally south, varied its direction considerably more than did Sharks M89-2 and M89-3. These last two sharks both travelled in a fairly direct westerly direction. Sharks M89-1 and M89-2 averaged $1\cdot33$ km $h^{-1}$ over the tracking period (Fig. 3). Shark M89-3 travelled nearly twice as far as the others, averaging $2\cdot55$ km $h^{-1}$. The rate of movement in the first hour of tracking exceeded $1\cdot80$ km $h^{-1}$ for all three fish. M89-1 and M89-2 both slowed considerably in the first few hours after release, whereas M89-3 first increased its speed to nearly $4\cdot44$ km $h^{-1}$ before slowing to $2\cdot77$ km $h^{-1}$. The average rate of movement for all three fish was lowest during the early to mid-morning hours. One shortfin mako shark (about the same size as our fish) tracked off the eastern coast of the USA averaged about $3\cdot70$ km $h^{-1}$ without any apparent change in swimming pattern, although it did reach $5\cdot55$ km $h^{-1}$ for a short time (F. Carey, personal communication). White sharks, *Carcharodon carcharias*, tracked off southern Australia averaged $3\cdot2$ km $h^{-1}$ (Strong *et al.* 1992).

Satellite images of sea surface temperatures (SSTs) were obtained for each track. Several temperature breaks and current eddies of 1°C to 2°C were present in and around the islands of the southern California bight. The SST image associated with the track of Shark M89-1 was obscured by clouds. The track of Shark M89-2 stayed on the warm side of a 2°C temperature break as the fish moved west toward the Avalon Bank. The track of Shark M89-3 crossed two temperature gradients as the fish moved from warmer water off La Jolla, California, to water 2°C to 3°C cooler as it moved west. Neither of these two sharks showed any sign of changing their behaviour in response to SSTs as did the striped marlin tracked earlier in the same area (Holts and Bedford 1990).

### *Vertical Distribution and Temperature Preferences*

A major feature of this study is that the three juvenile shortfin mako sharks observed in the southern California bight oriented to the surface waters above the thermocline. They spent 90% of the total tracking time in the mixed layer above 20 m. Slightly more daylight hours than night-time hours were spent below 20 m (Fig. 3).

The track of Shark M89-1 showed considerably more vertical activity than did the tracks of the other two sharks. M89-1 spent most of the night-time hours in continual vertical excursions between 2 and 15 m. The frequency of excursions slowed considerably after sunrise, although activity remained high through the end of the tracking period. Tracks from M89-2 and M89-3 showed fewer vertical excursions, but several of these lasted 1 h or longer. Vertical excursions of M89-1 and M89-2 were greatest during the night, whereas M89-3 was most active during the mid-morning period of the second day. These sharks did not descend below 25 m during the night-time hours, and, excluding the post-tagging plunge, only one (M89-3) descended below 25 m during the day.

Depth of the thermocline averaged 14–16 m during the first track and 19 to 20 m during the second and third. In all tracks, the mixed layer was 20°C to 21°C and the steepest gradient in the thermocline occurred from 18°C to 20°C. The total time that all three sharks spent in the mixed layer was 81·6%, with another 11·4% spent in the 18°C to 20°C transition zone (Table 1). Only infrequent or short excursions below the thermocline occurred, and there was little difference between day and night. Only vaguely apparent in this study were patterns observed for blue and shortfin mako sharks in the Atlantic. Those sharks made their longest excursions and deeper dives during the day and smaller vertical excursions at night. In that study, a large female shortfin mako shark spent most of the time well below the mixed layer and reached depths greater than 400 m several times (Carey and Scharold 1990). Our sharks were smaller than the shortfin mako and blue sharks tracked by Carey and Scharold (1990). The reason for observed differences in depth preference is unknown, although condition, age and location may all be involved.

Several other pelagic predators prefer the warmer water of the mixed layer, including the blue shark (Sciarrotta and Nelson 1977) and the striped marlin (Holts and Bedford 1990). Still others, including the white shark (Carey *et al.* 1982) and the yellowfin tuna, *Thunnus albacares* (Carey and Olson 1982; Yonemori 1982), orient to the steepest gradient of the thermocline.

**Table 1. Percentages of time spent at different temperatures during day (D) and night (N) for shortfin mako sharks**

| Temperature (°C) | Shark M89-1 | | Shark M89-2 | | Shark M89-3 | | Combined | | Total |
|---|---|---|---|---|---|---|---|---|---|
| | D | N | D | N | D | N | D | N | |
| 20–21 (mixed layer) | 75·4 | 86·3 | 65·3 | 79·8 | 74·3 | 100·0 | 73·3 | 88·4 | 81·6 |
| 18–19 | 9·9 | 10·6 | 22·1 | 20·2 | 10·8 | — | 12·3 | 10·3 | 11·4 |
| 17–18 | 1·3 | 1·2 | 5·9 | — | 0·6 | — | 1·8 | 0·5 | 0·6 |
| 16–17 | 4·8 | 0·8 | 6·5 | — | 5·6 | — | 5·3 | 0·3 | 2·8 |
| 15–16 | 2·3 | 0·7 | 0·2 | — | 0·9 | — | 1·4 | 0·3 | 0·3 |
| 14–15 | 3·0 | 0·4 | — | — | 0·8 | — | 1·6 | 0·2 | 0·9 |
| 13–14 | 1·5 | — | — | — | 7·0 | — | 3·4 | — | 1·7 |
| 12–13 | 1·8 | — | — | — | — | — | 0·9 | — | 0·7 |

### *Diel Patterns*

Neither horizontal nor vertical movements indicated any diel activity pattern common to all three sharks. Likewise, no pattern of movement such as a home range associated with the nearby islands, the banks or the shore was evident, probably owing to the diverse topography in the area. Sciarrotta and Nelson (1977) observed an island-oriented onshore–offshore movement in blue sharks associated with feeding. Interisland cruising and island patrolling were described for white sharks (Strong *et al.* 1992). The shortfin mako sharks tracked in the present study were not obviously orienting to any features. At this age, in the southern California bight, juvenile shortfin mako sharks may have an extensive home range as do shortfin mako sharks in the Atlantic (Casey and Kohler 1992). If this is the case, extended tracks of several days may be necessary to identify any diel activity patterns or island-oriented movements.

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**Abstract.**–Recruitment of individuals from the epipelagic phase to the demersal armorhead *Pseudopentaceros wheeleri* population at Southeast (SE) Hancock Seamount has typically been recognized by the influx of fish with a high fatness index (FI; body depth relative to fork length). Reliance on this index was dictated by the peculiarity of the seamount life history stage in which armorhead cease somatic growth soon after recruitment to the seamount and FI declines during seamount residence until death. Limited sampling opportunities and variability in FI at the time of recruitment preclude the exclusive use of FI as a means of identifying newly arrived recruits among recruits-of-the-year and hence the timing of annual recruitment. Settlement and recruitment to the seamount population are synonymous. Efforts to develop a method of identifying new recruits were initiated by an examination of epipelagic and seamount (SE Hancock) armorhead for differences in macroparasites as well as hepatosomatic and visceral fat-somatic indices. Of the two condition indices, the hepatosomatic index held the most potential but was considered too labile because prerecruits probably experience decreases that vary according to energetic demands during seamount migration. The monogenean gill parasite *Microcotyle macropharynx* was highly prevalent among seamount individuals in all sampling periods but absent from epipelagics. Based on probable rapid infection and maturation, identification of new recruits was based on the absence of mature *M. macrophaynx*. Results indicate that significant new recruitment occurred only during the late spring to midsummer sampling periods, and the mean FI of new seamount recruits was lower than that of comparable size epipelagics.

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# Use of a monogenean gill parasite and feasibility of condition indices for identifying new recruits to a seamount population of armorhead *Pseudopentaceros wheeleri* (Pentacerotidae)

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The armorhead *Pseudopentaceros wheeleri* (Hardy) in the North Pacific Ocean initially occupies an epipelagic and then demersal habitat during its life history. Progeny originate from winter spawning of the demersal armorhead population associated with the summit and upper slopes of the southern Emperor-northern Hawaiian Ridge (SE-NHR) seamounts (Fig. 1) (Bilim et al., 1978; Borets, 1979). Larvae are initially found in surface waters around the seamounts (Fedosova and Komrakov, 1975; Borets, 1979) but soon move or are advected into subarctic waters of the central and northeastern Pacific (Boehlert and Sasaki, 1988). Here they feed in oceanic surface waters and undergo somatic growth, accumulate energy reserves, but experience no reproductive development. These epipelagic individuals appear deep-bodied and display a striking pattern of blue and silver blotches along their dorsal and lateral regions. The process and timing by which epipelagic individuals recruit back to the SE-NHR seamounts is not well understood (Boehlert and Sasaki, 1988). Individuals are primarily 28–33 cm fork length (FL) upon recruitment to the SE-NHR seamounts (Humphreys et al., 1989). Since recruits are similar in length and co-occur among the resident seamount population, settlement and recruitment to the seamounts are considered synonymous events (Humphreys et al., 1989). Unlike the epipelagics, the seamount population is demersal and virtually uniform in length, but morphologically variable. Three morphological variants (the "fat," "intermediate," and "lean" morphotypes) were previously recognized and found to represent different stages of the demersal seamount phase (Humphreys et al., 1989). This variation intergrades from the deep-bodied, overall bluish-gray coloration of presumably recent recruits (fat morphotype) through progressively leaner forms of uniformly brownish coloration (intermediate and lean morphotypes). Relative body depth refers to the ratio of body depth at first anal spine to FL and hereafter is called the fatness index (FI; Somerton and Kikkawa, 1992). Usage of FI values recognizes that these variations form a continuum rather than discrete changes and has replaced classification by morphotype (Somerton and Kikkawa, 1992). Declining FI reflects the transformation by individuals as the elapsed time of seamount residence increases. During this phase, somatic growth ceases upon recruitment, and stored energy reserves are eventually mobilized for reproductive development and spawning. These processes contribute to the decline in FI and ultimately lead to death (Humphreys et al., 1989).

The discovery of large aggregations of armorhead over the summits and upper slopes of SE-NHR seamounts (Fig. 1) during exploratory work by the former Soviet Union in 1967–1969 (Komrakov, 1970) led to a full-scale bottom trawl fishery in this region by both Japanese and the former Soviet trawl fleet (Uchida and Tagami, 1984). By the end of 1975, the cumulative combined fleet catch of armorhead was some 880,000 metric tons (t). Total annual catch of armorhead by the Japanese trawl fleet declined dramatically after 1976 (Humphreys et al., 1984) and continues to remain low throughout the SE-NHR region (R. Humphreys, unpubl. data). In 1977 the Hancock Seamounts, located in the southermost portion of the SE-NHR trawl fishery, came under U.S. jurisdiction with the implementation of the 200-mile fishery conservation zone (Humphreys et al., 1984). During 1978–1984, several Japanese trawlers were allowed to fish the Hancock Seamounts but were regulated by permit and an annual catch quota (Uchida and Tagami, 1984;

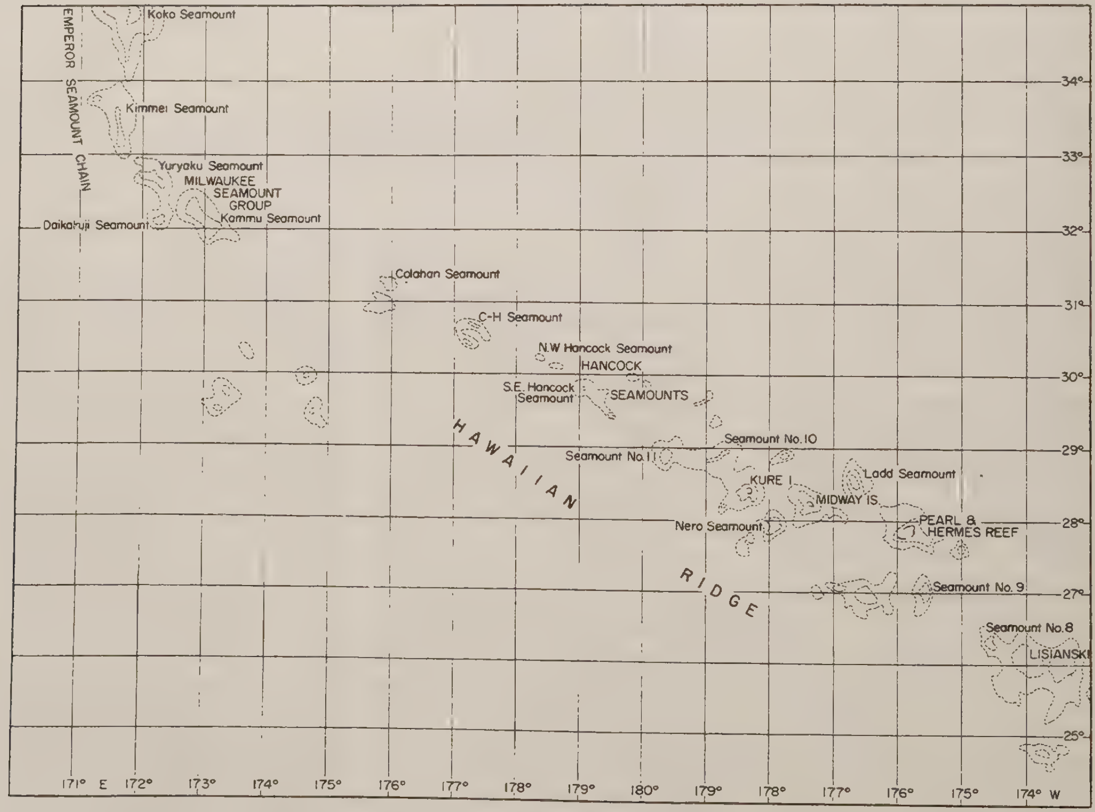
EMPEROR SEAMOUNT CHAIN
Koko Seamount
Kimmei Seamount
Yuryaku Seamount
MILWAUKEE SEAMOUNT GROUP
Kammu Seamount
Daikakuji Seamount
Colahan Seamount
C-H Seamount
N.W Hancock Seamount
HANCOCK SEAMOUNTS
S.E. Hancock Seamount
HAWAIIAN RIDGE
Seamount No. 10
Seamount No. 11
KURE I.
Ladd Seamount
MIDWAY IS.
Nero Seamount
PEARL & HERMES REEF
Seamount No. 9
Seamount No. 8
LISIANSKI
34°
33°
32°
31°
30°
29°
28°
27°
25°
171° E
172°
173°
174°
175°
176°
177°
178°
179°
180°
179°
178°
177°
176°
175°
174° W

Figure 1

The major habitat of dermersal armorhead is located over the southern Emperor-northern Hawaiian Ridge (SE-NHR) seamounts extending from Koko Seamount to the northwest down through the Hancock Seamounts in the southeast region.

Somerton and Kikkawa, 1992). Owing to sustained low annual catches at the Hancock Seamounts, the National Marine Fisheries Service (NMFS) Honolulu Laboratory implemented both a research stock assessment program in 1985 and recommended institution of a moratorium (in effect since 1986) prohibiting trawl fishing at the Hancock Seamounts (Somerton and Kikkawa, 1992). The remainder of the SE-NHR seamounts, which represent some 90% of the historical trawl fishery in terms of habitat and overall catch, lie in international waters and under no fishery management control. As increases in armorhead biomass at Hancock and other SE-NHR seamounts appear to depend exclusively on recruitment, recent work has focused on examining the temporal pattern of seamount recruitment and the biological characteristics of new recruits. Boehlert and Sasaki (1988) used monthly length-weight data recorded by the Japanese at four SE-NHR seamounts during May 1972–December 1973 to estimate the seasonality of recruitment. Assuming that new recruits have a condition factor of ≥2.0, they found recruitment highest during April–May 1973 and secondary peaks in August 1972 and July 1973. Annual recruitment to Southeast (SE) Hancock Seamount, one of two guyots composing the Hancock Seamounts, was sporadic between 1978 to 1990. Strong recruitment (≥50% of population biomass) at SE Hancock Seamount occurred only in 1980 and 1986, and moderate recruitment (ca. 20–30% of population biomass) in 1988 and 1990, based on catch per unit of effort (CPUE) and FI distributions derived from Japanese trawl data and NMFS stock assessment surveys (Somerton and Kikkawa, 1992).

Little further progress, however, has been made in discerning the timing of recruitment and biological characteristics of newly arrived recruits. The apparent temporal variability in recruitment, the change in FI during time elapsed between recruitment and sampling, coupled with limited sampling opportunities, make the identification and study of new recruits and their temporal recruitment pattern problematic. A potential alternative for identifying newly recruited armorhead uses biological indicators to distinguish a new seamount arrival from longer resident armorhead. Parasites have been frequently used as biological indicators in fish and their benefit to studies of fish stock separation, movement, and diet are numerous (Williams et al., 1992). In relation to seamount studies, differences in the trematode parasite fauna of sablefish off Canada's west coast led Kabata et al. (1988) to surmise that seamount populations of sablefish are distinct and separate from those sablefish inhabiting the continental slope. Since seamount armorhead populations are derived from epipelagic individuals, we examined specimens of both life history phases for parasite differences and other distinguishing features. We report on the feasibility of using a monogenean gill parasite and two condition indices as potential indicators of new seamount recruits.

## Methods

Epipelagic specimens of *P. wheeleri* ($n = 53$) were incidentally captured from the central North Pacific (around lat. 45°N, long. 155°W) in July 1984 and 1985 and from the eastern North Pacific (around lat. 46°N, long. 129°W) in July 1985 by the Japanese fishing vessels *Oshoro Maru* and *Tomi Maru No. 88*, respectively, during salmon longline and surface drift gillnet operations. These specimens were saved intact and stored frozen prior to examination. Specimens of seamount armorhead ($n = 1{,}220$) were collected from the southern end of the SE-NHR at SE Hancock Seamount (29°48'N, 179°04'E; see Fig. 1) by bottom longline gear during research cruises of the NOAA ship *Townsend Cromwell* in June 1985, August and October 1986, April and August 1987, and January, July, August, and November 1988. All seamount specimens were derived from efforts beginning in 1985 to estimate armorhead relative abundance (catch per unit of effort) at SE Hancock Seamount by using standardized assessment techniques described in Somerton and Kikkawa (1992). Seamount specimens were either saved intact and stored frozen, or gills and viscera were removed and preserved at sea in either alcohol-formalin-acetic acid (AFA) solution or placed in a dilute (0.0004%) formalin solution for several hours and then preserved in 10% formalin. Collection data for armorhead specimens included body weight, FL, body depth at first anal spine, sex, and date and location of capture. Measurements were made to the nearest millimeter, and body weight to nearest gram.

Under a dissecting microscope, the gill arches and visceral organs of armorhead specimens were examined for macroparasites. Guidelines proposed by Sindermann (1983) were followed to determine which species have potential as biological tags. Ideal parasite characteristics include ease of detection and identification, a single host-life cycle, and temporal stability in prevalence. Furthermore, the parasite should persist in the host during the study, and prevalence should differ significantly between study areas. These criteria were best fulfilled by the monogenean *Microcotyle macropharynx* (Mamaev), based on examinations of the seven parasite taxa (monogenean *Trochopus* sp., digenean *Bivesicula* sp., larvae of the nematode *Anisakis* type I, nematode *Hysterothylacium* sp., an unidentified caligoid copepod, and juveniles of an unidentified gnathiid isopod) found in the epipelagic and seamount armorhead collected in June 1985 and August 1986. Subsequent examinations of armorhead were restricted to the gills where *M. macropharynx* were exclusively found. Specimens of *M. macropharynx* were readily distinguished from *Trochopus* sp. by the disk-shaped opisthaptor of the latter monogenean. All specimens of *M. macropharynx* were initially identified as that of *M. sebastis* though the pharynx of these specimens appeared to be unusually large[1]. During the review process, a new species description (Mamaev, 1989) of the monogenean *M. macropharynx* collected in 1969–70 from *P. richardsoni* (=*P. wheeleri*) in the Hawaiian Islands region was brought to the attention of the senior author. Subsequently specimens initially identified as *M. sebastis* were re-examined and all found to be *M. macropharynx*[2]. The large pharynx (in relation to the anterior suckers) of *M. macropharynx* distinguishes this species from all other species of *Micocotyle* (Mamaev, 1989). Each *M. macropharynx* was staged as either immature or potentially mature, based on absence or development of the paired yolk ducts, respectively. These organs are the last to develop before egg development in the related species *M. sebastis* (Thoney, 1986). All parasite taxa were saved and stored in 70% ethyl alcohol. Prevalence and mean intensity of *M. macropharynx* in seamount armorhead were computed for each sampling period. Following the terminology defined in Margolis et al. (1982), prevalence (expressed as a percentage) refers to the number of host species infected with a particular parasite species, divided by the number of hosts examined; and mean intensity is derived by dividing the total number of a particular parasite species by the number of individual hosts infected by that parasite. Prevalence and mean intensity data from seamount armorhead were partitioned into two FI groups of <0.26 and ≥0.26. This grouping is based on the observation that 0.26 was the lowest FI found for epipelagic armorhead in this study and thus a possible minimum FI for newly arrived seamount recruits.

Liver and visceral fat weights were also determined for the 27 epipelagic armorhead >27.5 cm FL (of comparable length to seamount individuals) and 410 seamount armorhead collected during October 1986 ($n$ = 115) and January ($n$ = 195), July ($n$ = 18), and November 1988 ($n$ = 82). Liver and visceral fat deposits were removed from the body cavity, blotted dry, and weighed to the nearest 0.1 g. Liver and visceral fat weights are expressed in relation to total body weight and referred to as the hepatosomatic index (HSI) and visceral fatsomatic index (VFSI), respectively. Data was arcsine transformed and tested for normality with the Lilliefor's method of the Kolmogorov-Smirnov test (Wilkinson, 1990). Sample means were compared by either $t$-test, or by Mann-Whitney test if samples remained nonnormal (Wilkinson, 1990).

Estimates of the proportion of recruits-of-the-year to the total SE Hancock armorhead population during each sampling period were based on stock-assesssment-derived FI distributions of the armorhead population. That proportion of the FI distribution ≥0.26 were considered recruits-of-the-year. Data and procedures used to calculate the population FI distribution are presented in Somerton and Kikkawa (1992). The proportion of recruit-of-the-year armorhead in each sampling period un-infected by mature stages of *M. macropharynx* was estimated from results of the prevalence data for those armorhead (from samples examined for *M. macropharynx*) with a FI ≥0.26.

## Results

*Microcotyle macropharynx* were not present in any of the 53 epipelagic armorhead examined but were present in all 775 seamount armorhead with FI <0.26 and in 417 (93.7%) of 445 specimens with FI ≥0.26. Among seamount armorhead with FI <0.26, both the combined (irrespective of maturity stage) category and the immature and mature stage of *M. macropharynx* were highly prevalent (>75%) in all nine sample periods surveyed (Table 1). A similar pattern of high *M. macropharynx* prevalence was found among the seamount armorhead with FI ≥0.26 although instances of lower prevalence appear during the two earliest sample periods (Table 1). Mean intensity of immature *M. macropharynx* in both FI groups was considerably lower in each sample period than the corresponding mean intensities of the mature stage and combined category (Table 2). Mean intensity of mature stage *M. macropharynx* in each sample period and FI group was sufficiently high to ensure easy detection in armorhead infected with mature stage individuals of this monogenean. A wide range in sizes of *M. macropharynx*, including mature stages with eggs, was present among the gills of armorhead, indicating that this parasite has a monoxenous life cycle.

Seamount armorhead without mature *M. macropharynx* represented 5.2% (64) of the 1,220 fish examined. Among those seamount armorhead found un-

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[1] R. R. Payne, Department of Biological Sciences, Biola Univ., La Mirada, CA, personal commun. 1988.

[2] R. R. Payne, Department of Biological Sciences, Biola University, La Mirada, CA, pers. commun. 1992.

**Table 1**

Prevalence of the monogenean *Microcotyle macropharynx* in the gills of armorhead *Pseudopentaceros wheeleri* by fatness index (FI) groups of <0.26 and ≥0.26, collected from Southeast Hancock Seamount during 1985–88. Within each FI group, prevalence is further categorized by maturity stage of monogenean or regardless of (combined). Prevalence expressed as a percentage of total number (*n*) of armorhead examined. Differences in (*n*) between maturity stages indicates missing data. Occurrences of combined (*n*) exceeding (n) of both maturity stages represents instances where monogeneans from an additional sample were not staged.

| | FI <0.26 | | | FI ≥0.26 | | |
|---|---|---|---|---|---|---|
| Sample period | Immature stage | Mature stage | Combined | Immature stage | Mature stage | Combined |
| Jun 1985 | 98.0 | 95.9 | 100.0 | 70.0 | 45.0 | 80.0 |
| | *n*=49 | *n*=49 | *n*=50 | *n*=20 | *n*=20 | *n*=20 |
| Aug 1986 | 93.0 | 100.0 | 100.0 | 68.8 | 66.7 | 75.0 |
| | *n*=57 | *n*=57 | *n*=58 | *n*=48 | *n*=48 | *n*=48 |
| Oct 1986 | 92.5 | 100.0 | 100.0 | 84.9 | 96.2 | 99.1 |
| | *n*=80 | *n*=80 | *n*=80 | *n*=106 | *n*=106 | *n*=107 |
| Apr 1987 | 80.6 | 100.0 | 100.0 | 85.2 | 96.3 | 96.3 |
| | *n*=134 | *n*=137 | *n*=137 | *n*=27 | *n*=27 | *n*=27 |
| Aug 1987 | 88.2 | 100.0 | 100.0 | 95.8 | 89.6 | 95.8 |
| | *n*=68 | *n*=68 | *n*=68 | *n*=48 | *n*=48 | *n*=48 |
| Jan 1988 | 94.5 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 |
| | *n*=181 | *n*=183 | *n*=183 | *n*=12 | *n*=12 | *n*=12 |
| Jul 1988 | 93.3 | 100.0 | 100.0 | 78.8 | 80.8 | 90.4 |
| | *n*=45 | *n*=45 | *n*=45 | *n*=52 | *n*=52 | *n*=52 |
| Aug 1988 | 93.6 | 100.0 | 100.0 | 90.4 | 78.8 | 94.2 |
| | *n*=47 | *n*=47 | *n*=47 | *n*=52 | *n*=52 | *n*=52 |
| Oct–Nov 1988 | 96.6 | 97.7 | 100.0 | 98.7 | 97.5 | 100.0 |
| | *n*=87 | *n*=87 | *n*=87 | *n*=79 | *n*=79 | *n*=79 |

**Table 2**

Mean intensity of the monogenean *Microcotyle macropharynx* in the gills of armorhead *Pseudopentaceros wheeleri* by fatness index (FI) groups of <0.26 and ≥0.26, collected from Southeast Hancock Seamount during 1985–88 Within each FI group, mean intensity is further categorized by maturity stage of monogenean or regardless of (combined). Sample size from which mean intensity is based on is denoted by (*n*). Differences in (n) between maturity stages indicates missing data. Occurrences of combined (*n*) exceeding (n) of both maturity stages represents instances where monogenean was present but stage of maturity not determined. Smaller sizes of (n) in this table compared to the (*n*) of corresponding cells in Table 1 indicates instances where data on prevalence, but not mean intensity, is available.

| | FI <0.26 | | | FI ≥0.26 | | |
|---|---|---|---|---|---|---|
| Sample period | Immature stage | Mature stage | Combined | Immature stage | Mature stage | Combined |
| June 1985 | 12.23 | 35.72 | 52.06 | 4.64 | 95.22 | 57.63 |
| | n=48 | *n*=47 | *n*=50 | *n*=14 | *n*=9 | *n*=16 |
| Aug 1986 | 9.09 | 63.84 | 72.12 | 6.91 | 30.41 | 34.03 |
| | *n*=53 | *n*=57 | *n*=58 | *n*=33 | *n*=32 | *n*=36 |
| Oct 1986 | 9.74 | 88.01 | 97.03 | 5.42 | 65.77 | 68.18 |
| | *n*=74 | *n*=80 | *n*=80 | *n*=90 | *n*=102 | *n*=106 |
| Apr 1987 | 16.21 | 65.17 | 79.92 | 19.23 | 162.86 | 181.14 |
| | *n*=79 | *n*=24 | *n*=24 | *n*=13 | *n*=14 | *n*=14 |
| Aug 1987 | 17.97 | 58.48 | 75.48 | 14.42 | 58.21 | 72.68 |
| | *n*=31 | *n*=33 | *n*=33 | *n*=19 | *n*=19 | *n*=19 |
| Jan 1988 | 15.84 | 56.66 | 71.11 | 20.44 | 110.00 | 130.44 |
| | *n*=31 | *n*=35 | *n*=35 | *n*=9 | *n*=9 | *n*=9 |
| Jul 1988 | 14.47 | 27.69 | 41.25 | 7.67 | 36.47 | 37.80 |
| | *n*=30 | *n*=32 | *n*=32 | *n*=18 | *n*=17 | *n*=20 |

infected by mature stage *M. macropharynx*, virtually all were of a FI ≥0.26 (Table 3). The four armorhead with FI <0.26 and uninfected by mature *M. macropharynx* had FI values disjunct from similarly un-infected armorhead with FI ≥0.26 (Fig. 2). Mean FI's of the seamount armorhead group (FI ≥0.26) without mature *M. macropharynx* ($x$ = 0.291) and the epipelagic group ($x$ = 0.307) were significantly different (*t*-test, $P < 0.001$). From samples of seamount armorhead (FI ≥0.26) examined for prevalence of mature stage *M. macropharynx*, the percentage of those found without mature *M. macropharynx* was higher in the June–August samples (Table 3). However, these latter results did not always correspond with peaks in the proportion of the seamount armorhead population (with FI ≥0.26) obtained from stock assess-

**Table 3**

Percent absence of mature stages of the monogenean *Microcotyle macropharynx* from the gills of armorhead *Pseudopentaceros wheeleri* by fatness index (FI) groups of <0.26 and ≥0.26, sampled from Southeast Hancock Seamount during 1985–88. Sample size examined for each category denoted by (*n*).

| Sample period | FI <0.26 | FI ≥0.26 |
|---|---|---|
| Jun 1985 | 4.1 | 55.0 |
| | *n*=49 | *n*=20 |
| Aug 1986 | 0 | 33.3 |
| | *n*=57 | *n*=48 |
| Oct 1986 | 0 | 3.8 |
| | *n*=80 | *n*=106 |
| Apr 1987 | 0 | 3.7 |
| | *n*=137 | *n*=27 |
| Aug 1987 | 0 | 10.4 |
| | *n*=68 | *n*=48 |
| Jan 1988 | 0 | 0 |
| | *n*=183 | *n*=12 |
| Jul 1988 | 0 | 19.2 |
| | *n*=45 | *n*=52 |
| Aug 1988 | 0 | 21.2 |
| | *n*=47 | *n*=52 |
| Nov 1988 | 2.3 | 2.5 |
| | *n*=87 | *n*=79 |

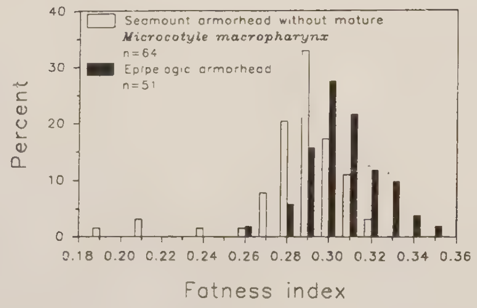

**Figure 2**

Distribution of fatness index for specimens of epipelagic and Southeast Hancock Seamount armorhead *Pseudopentaceros wheeleri* without mature parasites of *Microcotyle macropharynx*.

ment surveys (Fig. 3; data taken Somerton and Kikkawa (1992) from FI distributions for each sample period except November 1988).

Mean HSI ($x = 3.147$; Fig. 4) of the epipelagic group was significantly different from that of seamount armorhead with FI ≥0.26 ($x = 1.358$, Mann-Whitney test, $P < 0.001$) and those with FI <0.26 ($x = 1.028$, *t*-test, $P < 0.001$). Furthermore, none of the seamount armorhead except for two individuals in the FI ≥0.26 group had HSI values exceeding the lowest value (2.154) of the epipelagic group. Differences between the mean HSI of the two seamount FI groups were also highly significant (Mann-Whitney test, $P < 0.001$). Regardless of FI value, the difference in mean HSI between epipelagics and seamount armorhead without ($x = 1.744$, *t*-test, $P < 0.001$) and with ($x = 1.148$, *t*-test, $P < 0.001$) mature *M. macropharynx* remained significantly different, as were differences between the latter two groups (*t*-test, $P < 0.001$). The seamount armorhead group without mature *M. macropharynx* exhibited the least overlap in HSI values with other seamount groups (Fig. 4).

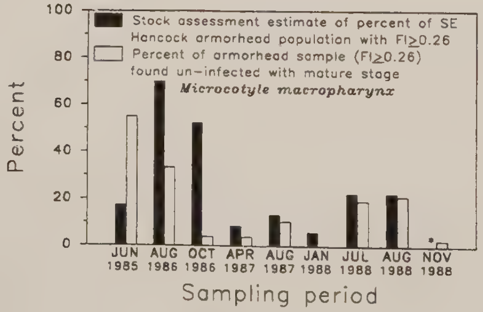

**Figure 3**

Percent of armorhead *Pseudopentaceros wheeleri* samples (fatness index (FI) ≥0.26) without mature *Microcotyle macropharynx* (from Table 3), and the percent of SE Hancock armorhead population with FI ≥0.26; the latter estimated from stock assessment surveys during each of the periods (except November 1988) where armorhead were sampled for *M. macropharynx* infection.

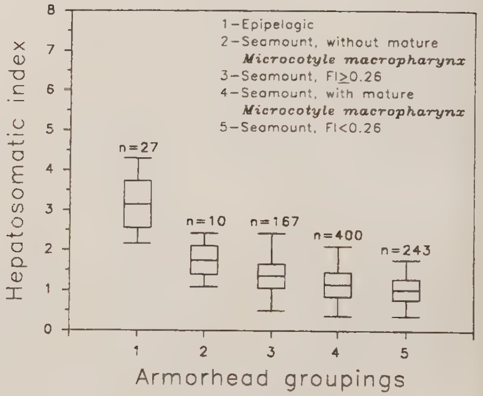

**Figure 4**

Hepatosomatic index by each grouping of armorhead *Pseudopentaceros wheeleri*. The mean is indicated by the midpoint horizontal line within each box, one standard deviation about each mean is denoted by the box, and the range is displayed as the horizontal lines above and below the box.

For the epipelagic group, mean VFSI ($x = 2.152$; Fig. 5) was significantly different from seamount armorhead with FI ≥0.26 ($x = 3.580$, *t*-test, $P < 0.001$) and those with FI <0.26 ($x = 2.933$, Mann-Whitney test, $P = 0.007$). Mean VFSI differences between the latter two seamount groups were also significant (Mann-Whitney test, $P < 0.001$). The mean VFSI of the epipelagic group was also significantly different from that of seamount armorhead with ($x = 3.185$, Mann-Whitney test, $P < 0.001$) and without ($x = 3.663$, *t*-test, $P = 0.009$) mature *M. macropharynx*, whereas the latter two seamount groups did not significantly differ in mean VFSI (Mann-Whitney, $P = 0.364$). Overlap in VFSI among the various groups (Fig. 5) was substantially greater than exhibited for HSI.

## Discussion

The complete absence of the monogenean *M. macropharynx* from all epipelagic armorhead exam-

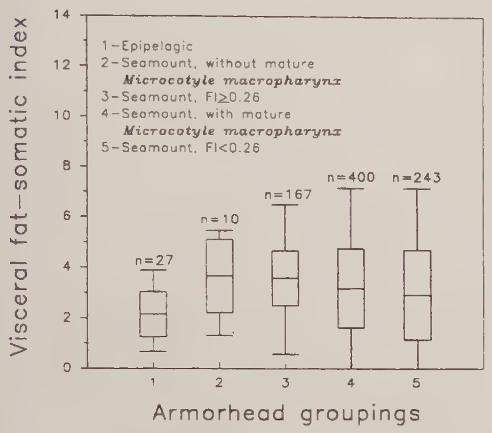

**Figure 5**

Visceral fat-somatic index by each grouping of armorhead *Pseudopentaceros wheeleri*. The mean is indicated by the midpoint horizontal line within each box, one standard deviation about each mean is denoted by the box, and the range is displayed as the horizontal lines above and below the box.

ined, and its high prevalence among seamount armorhead during all sample periods, support the notion that infestation of this parasite originates at the seamount. The prevalence of immature *M. macropharynx*, particularly for those armorhead with FI <0.26, indicates that infestation at the seamount is probably a continuing process. The presence of *M. macropharynx* in all 775 seamount armorhead with FI of <0.26 also negates the likelihood of a sizable proportion of seamount armorhead becoming uninfested over time.

The maturation rate of *M. macropharynx* on armorhead remains undetermined, but Thoney (1986) has found the oncomiracidia of the morphologically similar *M. sebastis* capable of maturing within 12 days on the gills of black rockfish *Sebastes melanops* (Girard) off northern California. Although armorhead are different hosts, inhabit greater depths, and are geographically distant from black rockfish, the temperature range (12°–17°C) used by Thoney (1986) to determine the maturation time of *M. sebastis* is similar to that found on the summit and upper slope of SE Hancock Seamount. Assuming this rapid maturation also occurs among *M. macropharynx* infecting armorhead, we propose that armorhead with exclusively immature *M. macropharyx* have probably only recently become infested and have seamount residence times that differ little from those of uninfested armorhead. The 0.26 FI value may represent a lower FI limit for potential new recruits, for only 6% of seamount armorhead without mature *M. macropharynx* had FI values <0.26 and the lowest FI value of the epipelagics examined was 0.26. However, an unknown proportion of armorhead with FI ≥0.26 perhaps recruit during the previous year at sufficiently high FI values that these FI values still remain above 0.26 when sampled the following year. Even in this situation, such individuals would be infected with mature *M. macropharynx* by the time they are sampled the following year and therefore not mistaken for new recruits. The presence of *M. macropharynx* probably cannot identify recruits that arrived one or several months before sampling if initial infection occurs soon after recruitment and *M. macropharynx* mature some two weeks thereafter. Hence, our technique can detect only new recruits among the recruit-of-the-year population and is therefore limited to determining whether recruitment is a continuous process.

Of the two condition indices, VFSI shows little promise as an indicator of new recruits, for the VFSI values in epipelagic and seamount individuals broadly overlap, regardless of FI and the presence or absence of mature *M. macropharynx*. Conversely, virtually no overlap in HSI values occurs between epipelagic individuals and any of the seamount armorhead groupings. Preliminary results of sagittal otolith increment enumeration on epipelagic individuals (>27.5 cm FL) and SE Hancock armorhead without mature *M. macropharynx* indicates a common age around 2.5 years (R. Humphreys, unpubl. data). This appears to suggest that those epipelagic individuals examined either remain pelagic or represent "strays" who will eventually or have begun a delayed movement that will result in recruitment to a SE-NHR seamount but a protracted epipelagic phase. The higher mean HSI value of these epipelagics versus seamount armorhead (FI ≥0.26) un-infected by mature *M. macropharynx* suggests that HSI decreases somewhere during the period between movement to the seamounts and time of capture after seamount recruitment. To explain the higher mean HSI of epipelagics and evaluate its efficacy as a recruitment indicator, this forementioned period must be examined in relation to both time and distance.

Of the 27 epipelagic individuals with FLs comparable to seamount populations (>27.5 cm FL) and least distant from the SE-NHR seamounts, 22 were collected around lat. 45°N, long. 155°W; some 2,860 km northeast of the SE-NHR seamounts. Summertime captures of smaller (22–26 cm FL) epipelagics are also frequent from the above general location and indicate an age of some 1.5 years (Boehlert and Sasaki, 1988; R. Humphreys, unpubl. data). Since recruit-of-the-year seamount armorhead are age 2.5 years (R. Humphreys, unpubl. data), these smaller individuals apparently represent the year class which recruit to the SE-NHR seamounts in the following year. Allowing a one-year period (recruitment by the following summer) for individuals of the 1+ epipelagic year-class to move from the open ocean site (45°N 155°W) to the SE-NHR seamounts and also that the total distance traversed is twice the straight-line distance between these sites (assuming this is comparable to results of open-sea tracking of coho salmon *Oncorhynchus kisutch* reported in Ogura and Ishida (1992)), a rough estimate of the average ground speed required is 18 cm/s if currents are disregarded. Based on a length (27.1 cm FL) midway between the average FL of 1+ ($x$ = 24.49 cm FL) and 2+ year-old ($x$ = 29.64 cm FL) epipelagic specimens collected during summers at the open ocean site, individuals would need to swim 0.66 body length/s to arrive at an SE-NHR seamount one year later. This speed is close to the mean sustained cruising speeds (0.2–0.5 body length/second) typical of horizontally migrating fish (Beamish, 1978). Since no evidence exists of gonadal maturation in the epipelagic stage (Humphreys et al., 1989), the major energy demand during seamount migration is likely locomotion, in addition to basal metabolism. It is unknown whether feeding occurs during this migration; however, McKeown (1984) suggests that even if fish species feed during migration, the added energy intake may be negated by the additional energy required for feeding activity. Regardless of feeding, lipid reserves are typically used during migration (McKeown, 1984), and their storage in the liver and muscle makes these prime sites from which energy reserves can be drawn (Woodhead, 1975). As such, the liver is susceptible to net decreases in weight by the end of migration; an example of this occurs among migrating Barents Sea cod *Gadus morhua* (Woodhead, 1975). Evidence of fewer prey contents among higher FI armorhead examined at SE Hancock[3] indicates that recent recruits initially may feed little at the seamounts. This suggests that the liver remains susceptible to continued energy depletion and therefore continued decrease in liver weight. Assuming that liver weight is declining relatively faster than body weight, the HSI will not only decrease by the time of initial recruitment to the seamount but perhaps also during the interval between initial recruitment and sampling. Therefore, an annual or seasonal change in mean HSI among new recruits may be caused by inter- or intra-annual differences experienced by epipelagics in terms of environmental conditions and distance traversed during the seamount migration, along with an unknown time gap between initial recruitment and sampling. Hence, using HSI as a recruitment indicator appears to be inherently more labile and thereby less feasible and reliable than the method based on the absence of mature *M. macropharynx*.

The parasite approach revealed that new recruitment coincided primarily with the late spring and midsummer sampling periods. Somerton and Kikkawa (1992) have analyzed the recruitment patterns of armorhead to SE Hancock, using the modal progression of FI in which separate modes are considered annual cohorts. If a modal influx of high FI fish represents a "recruitment cohort," estimated recruitment was highest in terms of biomass (58 t) and percentage (79%) of the SE Hancock population during August and October 1986, whereas the next highest recruitment (8 t and 21% of the population, respectively) in July and August 1988 was comparatively modest. Interestingly, however, the level of new recruitment, as determined by the percentage of sampled armorhead (FI ≥0.26) un-infected with mature *M. macropharynx*, was highest in June 1985 and very low in October 1986. These results appear contrary to stock assessment based estimates of modest and high proportions of recruit-of-the-year armorhead (FI ≥0.26) in the seamount population during June 1985 and October 1986, respectively (see Fig. 2). These results can be reconciled if we consider that the rate of post-recruitment decline in FI (estimated at 0.00169/month; Somerton and Kikkawa (1992)) does not allow one to decipher between recruits which may have just arrived and those which arrived months prior to sampling. The absence of mature stage *M. macropharynx* appears to be the only criteria examined in this study capable of detecting whether a recruit-of-the-year (FI ≥0.26) is a new arrival to the seamount. Based on this criteria, the level of new recruitment during the months sampled was highest in June, less so in July and August, and very low during October, November, January, and April. These results tend to corroborate evidence of similar seasonal armorhead recruitment at other SE-NHR seamounts (Boehlert and Sasaki, 1988).

Recruits identified via the parasite approach typically have FI values ≥0.26 ($x$ = 0.291). However, a high FI value alone provides no assurance that an individual is a new recruit. The difference in mean FI between epipelagic individuals and new recruits (uninfected with mature *M. macropharynx*) may indicate that FI decreases sometime before epipelagics of recruitment size reach the seamounts. This can be adequately examined only after both groups are further sampled.

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[3] M. P. Seki, NMFS Honolulu Laboratory, pers. commun. January 1992.

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# ICHTHYOPLANKTON METHODS FOR ESTIMATING FISH BIOMASS INTRODUCTION AND TERMINOLOGY

*J. R. Hunter and N. C.-H. Lo*

The biomass of a fish stock can be estimated from the abundance of its spawn. This idea, first proposed by Hensen and Apstein (1897), has led to the development of ichthyoplankton methods currently used around the world to estimate biomass, and monitor trends in fish abundance. In recent years, ichthyoplankton based approaches have become more important because of increased demands for fishery-independent information. Five ichthyoplankton based methods for biomass estimation were described in this symposium: annual egg production method (AEPM), annual larval production method (ALPM), daily egg production method (DEPM), daily fecundity reduction method (DFRM), and egg deposition method (EDM). A variety of inexpensive ichthyoplankton indices of fish abundance was also described.

The AEPM (Saville, 1964) was the only ichthyoplankton method for estimating biomass until the 1980's. In the AEPM, biomass is computed from annual estimates of egg production and the potential annual fecundity of females. Eggs collected in plankton tows over the entire spawning season are used to calculate annual egg production. Annual fecundity per unit weight is calculated from the number of advanced yolked oocytes in ovaries of females taken just prior to spawning season.

$$B = P_aA/ER \qquad (1)$$

where B is the biomass for area A, $P_a$ is the annual egg production per unit sea surface area, A is area size, E is the total (annual) fecundity per unit weight of female, and R is the female fraction of the biomass (sex ratio). An important assumption of the AEPM is that potential annual fecundity is determinate, that is, fecundity becomes fixed prior to the beginning of the spawning season. The paper by Picquelle and Megrey on Alaskan pollock, is an example of the AEPM from this symposium.

Determinate fecundity seems to be common in boreal species such as herring and pollock but a common error is to assume that potential annual fecundity is fixed in all fishes. It became apparent in the 1970's and 1980's that the AEPM could not be used for the temperate species such as northern anchovy, queen fish, and tropical tunas because the standing stock of advanced oocytes in the ovary was not equivalent to annual fecundity. For example, female anchovy spawn 10 to 20 times per year, but the number of yolked oocytes in the ovary never exceeded those needed for 1 to 3 spawnings (Hunter and Leong, 1981). Thus, annual fecundity in anchovy is indeterminate and cannot be estimated by counting the standing stock of advanced oocytes in the ovary.

An alternative method, the DEPM, was developed for fishes like northern anchovy that have indeterminate annual fecundity (Lasker, 1985). In the DEPM, biomass estimates are based on daily, rather than annual, fecundity. Daily egg production was calculated from numbers of staged eggs taken in plankton samples. The relationship between daily spawning of eggs and spawning biomass was determined from the fraction of females spawning per day and batch fecundity:

$$B_s = P_0A/(R/W_f)SF \qquad (2)$$

where $B_s$ is the spawning biomass for area A, $P_0$ is the daily egg production at age 0 day per unit sea surface area, $W_f$ is average female weight, S is the fraction of females spawning per day, F is the batch fecundity, and A and R are defined as in equation 1.

Since the publication of the DEPM for northern anchovy (Lasker, 1985), the method has been applied to a variety of fish stocks. These applications provide new perspectives and augment the basic method. In this symposium, Alheit reviews application of the DEPM to clupeoid fishes including Peruvian anchoveta and the Spanish sardine. He surveys the literature, much of which is not generally available, and examines the extent to which the basic parameters in equation 2 vary among stocks of anchovy and sardines. Somerton demonstrates that the DEPM can be used to measure weekly changes in biomass of nehu, a small tropical anchovy, that spawns every other day, and lives less than a year. Shelton, Armstrong, and Roel review the use of the DEPM in South Africa where it has been used to make annual estimates anchovy biomass since 1984. In South Africa, the DEPM has been integrated with an annual acoustic trawl survey for anchovy in a way that yields more precise biomass estimates at a modest increase in cost.

In addition to the DEPM and AEPM, three other biomass estimation procedures are presented in this symposium: the annual larval production method (ALPM); egg deposition method (EDM); and the daily fecundity reduction method (DFRM). All three are based on the assumption of determinate annual fecundity. Heath describes an application of the ALPM to herring and summarizes a large, and not generally available literature. Heath describes how the ALPM was used to monitor the remarkable recovery of European herring stocks. The EDM for Pacific herring described by Schweigert is interesting because plankton samples were not used, instead, divers measured the density and area of spawn on the bottom. Pacific herring spawn in intertidal and subtidal zones where their sticky eggs adhere to algae or the substrate. The spawning grounds are easily found because of the clouds of milt produced during spawning.

The last method of biomass estimation considered in the symposium is the DFRM (Lo et al., 1992). This is a new daily method, that has yet to be formally tested as a management tool. The DFRM is designed to estimate the biomass of fish that spawn more than once per season but have determinate annual fecundity. It does not require measurement of batch fecundity and spawning frequency as do other daily methods. Instead, DFRM uses the daily decline in total fecundities to measure daily population fecundity.

$$B = P_0A/(R/W_f)D = P_0A/K \qquad (3)$$

where B is the biomass for area A, $P_0$ is the daily production of eggs per 10 $m^2$ sea surface, K is daily population fecundity = $(R/W_f)D$, in eggs/body weight/day, $D = d(E \cdot G)/dt$, the daily fecundity per female, E is the total number of advanced oocytes present in the ovary at time t (before spawning, E in equations 1 and 3 are equal), G is the fraction of females that have active ovaries at time t, and R and W are defined as before. If the spawning season is long, the fecundity reduction method requires less ship time than annual method since data from only a portion of the spawning season are needed.

Selection of the optimal ichthyoplankton-based method for biomass estimation is dependent upon a variety of factors including the spawning habits of the parents, whether annual fecundity is determinate or indeterminate, the level of precision desired, costs, and availability of other information. Two symposium papers consider biological issues related to the selection of methods. Zeldis reviews the reproductive biology of three New Zealand fishes: snapper, orange roughy, and hoki, and identifies what he believes to be the optimal ichthyoplankton method for each. Priede and Watson compare estimates of biomass of Atlantic mackerel using the AEPM and DEPM. The calculations for each method use the same ichthyoplankton data but different fecundity data. The results are surprising, because the two methods yielded biomass estimates that differed by only 16%. The estimates may have been similar because oocytes as small as 0.13 mm in diameter were included in the potential annual fecundity of mackerel. If only advanced yolked oocytes were included, the annual fecundity would have been much lower, and, consequently, the biomass based on the AEPM would have been much higher than the one based on the DEPM.

Ichthyoplankton data can be used to monitor trends in relative abundance of marine fishes as well as to estimate their actual biomass. Indices of relative abundance based on ichthyoplankton data are not corrected for variation in population fecundity, and consequently, are less costly and less precise than biomass estimates we have discussed thus far. Although no correction for population fecundity is made, indices may be adjusted for growth and mortality of larvae, or in the simplest case, may be simply the standing stock of larvae or eggs. Regardless of computational details, larva indices are surprisingly sensitive to major changes in stock abundance. For example, Scott et al. show that a larva index based on only 100 plankton samples distributed over 100,000 square miles of ocean can be used to follow major trends in the abundance of bluefin tuna. The possibility that a widespread stock such as bluefin tuna can be monitored with as few as 100 samples is certainly remarkable.

Why do simple ichthyoplankton indices of relative abundance work? Smith, explains that stock size and the area occupied by spawn are correlated, and that the presence and absence of larvae in plankton samples is an efficient measure of spawning area. Larva density, a more costly parameter to estimate precisely, has little importance in determining the size of the spawning area. Smith suggests larva density is of less consequence because most of the determinants of larva density, such rates as predation and starvation, are not related to the size of the spawning stock. In addition, in schooling fish, egg and larva density is probably related to school density which may not vary with biomass.

Many of the methods discussed in the symposium contain assumptions that could bias biomass estimates. Typical assumptions are that current year fecundity, egg mortality, larva mortality, and larva growth do not differ over time or among stocks. Estimates of egg or larva production were imprecise in some cases because the number of samples required for a precise estimate was too expensive to collect. The most precise estimates, in which all parameters are estimated in the same spawning season, have a coefficient of variation of 20 to 30%.

The estimation of the production of eggs ($P_0$) is straightforward and the lack of precision and potential biases are not usually the results of improper sampling or computational approach, but rather, reflect decisions based on costs. Smith makes some suggestions in regard to the frequency of biomass estimates and the precision of such estimates. He concludes that a precise annual estimate can seldom be justified in terms of fishery management and intervals longer than 1 year are more cost effective.

Fecundity estimates continue to be the Achilles heel of ichthyoplankton-based biomass estimation. Unlike estimates of egg or larva production, where procedures are standardized and well understood (Smith and Richardson, 1977), fecundity work may have a number of untested underlying assumptions which may be unsuspected or unspecified. AEPM and the DRFM require that the potential annual fecundity becomes fixed prior to spawning, but this assumption is not valid for all fishes and is seldom tested prior to application of annual methods.

Other typically untested assumptions underlying the annual method are that potential fecundity is equivalent to annual fecundity; females used to estimate potential annual fecundity have not spawned during the current reproductive season and all the oocytes that constitute the potential annual fecundity can be identified in samples. Procedures used to test these assumptions are described by Hunter et al. (1992). In the DEPM one must assume that batch fecundity, usually estimated from numbers of hydrated oocytes in the ovary, is equivalent to the number of eggs actually spawned and fertilized. To our knowledge, this assumption has never been tested. Usually some hydrated oocytes are retained in the lumen of the ovary and are not spawned, indicating that the correspondence between spawned eggs and hydrated oocytes is not exact.

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## DEFINITIONS

*Annual Egg Production Method (AEPM).*—Spawning biomass estimated from the ratio of the annual production of planktonic eggs to the potential annual fecundity of the stock.

*Annual Fecundity.*—The total number of eggs spawned by a female per year.

*Annual Larval Production Method (ALPM).*—Biomass estimated from the total annual production of larvae, estimated by back-calculating abundance at hatching from abundance at capture length and date, using estimates of growth and mortality rates, and integrated over the spawning area and period.

*Batch Fecundity.*—The number of hydrated oocytes released in one spawning; usually determined by counting the number of hydrated oocytes in the ovary.

*Daily Egg Production Method (DEPM).*—Spawning biomass estimated from the ratio of the daily production of planktonic eggs to the daily fecundity of the spawning population.

*Daily Fecundity.*—The number of eggs spawned per day per gram of fish in the population. In the DEPM it is calculated from the batch fecundity and daily spawning fraction of the stock, while in the DFRM it is calculated from the daily decline in standing stock of advanced oocytes.

*Daily Fecundity Reduction Method (DFRM).*—Biomass (vulnerable to trawls) estimated from the ratio of the daily production of planktonic eggs to the daily reduction in the total fecundity of the stock.

*Determinate Fecundity.*—Annual fecundity is determinate when the potential annual fecundity becomes fixed prior to the onset of spawning. In fishes with determinate fecundity, total fecundity decreases with each spawning because the standing stock of advanced yolked oocytes is not replaced during the spawning season.

*Egg Deposition Method (EDM).*—Spawning biomass estimated from measurement of the numbers of demersal eggs deposited on the bottom by demersally spawning fishes.

*Egg and Larva Indices of Abundance (ELIA).*—Use of the standing stock of eggs or larvae, or the area occupied by spawn, as an index of spawning biomass.

*Indeterminate Annual Fecundity.*—Annual fecundity is indeterminate when the potential annual fecundity of a female is not fixed prior to the onset of spawning and unyolked oocytes continue to be matured and spawned during the spawning season.

*Potential Annual Fecundity.*—Total number of advanced yolked oocytes matured per year, uncorrected for atretic losses. In species with determinate fecundity, potential annual fecundity is usually assumed to be equivalent to the total fecundity prior to the onset of spawning.

*Relative Fecundity.*—Fecundity divided by female weight.

*Total Fecundity.*—The standing stock of advanced yolked oocytes.

## OTHER SUGGESTED NOTATIONS

W: fish weight, $W_f$: female fish weight, $W_m$: male fish weight, L: fish length, $L_f$: female fish length, $L_m$: male fish length, V, $\sigma^2$: variance, $\bar{x}$: sample mean, SD: sample standard deviation, SE: sample standard error, COV: covariance, CV: coefficient of variation, *r*: correlation coefficient, $r^2$: coefficient of determination, T: temperature, df: degrees of freedom, z: instantaneous mortality rate and t: age.

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## PART 1. COASTAL PELAGIC FISHES
(*Report of Working Group 3*)

Edited by John R. Hunter and Tokio Wada

## PART 2. SUBARCTIC GYRE
(*Report of Working Group 6*)

Edited by Brent Hargreaves and Takashige Sugimoto

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# 1.0 INTRODUCTION

The objective of the Coastal Pelagic Fishes Working Group of PICES (see terms of reference) is to determine the characteristics of the environment, other than fishing, that affect the dynamics of the pelagic fish stocks of the North Pacific. Long term population changes, such as those that may be produced by global climate change, are of particular interest. Consequently, the research and related activities of the Group can be considered to be part of the GLOBEC International program of any PICES country.

The pelagic fishes currently considered by the Working Group are: Pacific herring, (*Clupea pallasi*); sardines (*Sardinops spp*); anchovies (*Engraulis spp*); mackerels (*Scomber spp, and Trachurus spp*); and saury (*Colorabis saira*). The world catch of these pelagic fishes in 1990 was 25 million tons. This catch was 35% of the world catch of marine fishes (Table 1). About 7 million tons of small pelagic fishes are taken annually in the North Pacific (FAO Statistical Areas 61, 67, and 77), with the Japanese sardine accounting for 65% of the total. Only a small portion of the world catch of small pelagic fishes are used directly for human consumption, most of the catch is reduced to fish meal and oil with the meal being an important ingredient of animal feeds. In Japan, where 80-90% of sardine and anchovy catch is used for meal, meal is used to support a rapidly growing fish aquaculture industry. Aquaculture production of fish in Japan, which has tripled between 1970 and 1990, could be seriously affected by a major decline in the Japanese sardine stock.

The general research approach of the Working Group is the comparative method. Our terms of reference state we are "to develop a program for a comparative study of the population dynamics and production of small pelagic fishes in the coastal ecosystem along the western and eastern continental margins of the North Pacific". Comparisons of the dynamics of marine animal populations can be used to test a variety of hypotheses. Comparisons of the same or similar species in different ecosystems can be used to assess effects of population response to different forcing variables (Bakun & Parrish, 1982). Alternatively, comparisons can be made of recruitment success of different species within the same ecosystem to identify specific patterns in the responses to basin-wide environmental change (Hollowed et al., 1987; Koslow, 1984).

**Variation in abundance**

Great variation in population size is characteristic of the major stocks of small pelagic fishes (Csirke, 1988). Considerable variability exists between species and regions. In Japanese waters, the catch of the sardine fluctuates over a two order of magnitude range while anchovy, mackerel, and saury are less variable (Table 2). In California, the same pattern emerges with the sardine population being much more variable than either anchovy or mackerel. Considering the differences in the data between Japan and California, the variability of the three stocks is remarkably similar in the two systems with the coefficient of variation for sardine about twice that for mackerel and with anchovy being roughly a third as variable as sardine. The most striking difference between the two systems is the much greater productivity of the Japanese stocks. On the average, landings of Japanese sardine, anchovy, and mackerel exceed the biomass of the equivalent California stocks.

The processes affecting the recruitment of year classes, and therefore population growth, have been researched for the last 20 years. This body of information on herring, anchovy and sardine, indicates that the recruitment success depends upon the survival of the early life history stages over the first 6 months of life with survivorship in the egg and larval stages being the most variable. Starvation as well as predation may be an important source of mortality during the first few weeks of life but thereafter survivorship is a function of larval growth and their size specific vulnerability to predators. Starvation and growth of early life history stages is fairly well documented but few quantitative estimates of predation exist.

A succession of strong or weak year classes over a decade or more are needed to realize the large and long fluctuations in population biomass, characteristic of many clupeoid populations. This pattern is also found in the physical oceanographic data where decadal periods of ocean climate exist (often called regimes) in which recruitment is either consistently lower or higher than the mean. In support of this argument authors point out correspondences between successions of strong or weak year classes and periods of lower or higher than average sea surface temperatures. How such temperatures affect recruitment remains obscure, however.

Persistent patterns in the success of year classes suggests to others that a positive feedback loop regulating population growth might exist, instead of the density-dependent negative feedback loop usually postulated as a regulatory mechanism. A positive feedback loop is possible in Japanese and California sardine since growth, migration, feeding habitats, and spawning habitats change as their populations grow. In the Japanese sardine energy allocation between growth and reproduction, egg and larval transport from spawning grounds to nursery grounds by the Kuroshio Current, may all be linked to population size. Thus, population response to changes in physical forcing variables may be modulated by internal population processes. Consequently, the long term effect of physical forcing variables on populations should be examined within the context of possible density dependent processes.

Lastly, it is important to recognize that these small pelagic fishes may be more closely linked to long term changes in primary and secondary production than are most other major stocks because they are planktivorous throughout their lives.

# 2.0 DESCRIPTIONS OF STOCKS

## 2.1 Eastern Pacific

### 2.1.1 California Sardine (*Sardinops sagax*)

Three stocks of sardine occur in the north eastern Pacific: a Gulf of California stock (Mexico); a southern Baja California stock (Mexico) [Punta Baja, Mexico to Cabo San Lucas]; and a northern stock (Punta Eugenia, Baja California, Mexico to Monterey, Alta California, USA). The northern stock, immortalized in Steinbeck's book, *Cannery Row*, has a summer feeding migration where fish migrate as far north as British Columbia, Canada.

In 1979, about 20 years after its near-total collapse, the northern stock showed the first signs of recovery. The beginning of the recovery is best illustrated by the average number of sardine eggs taken in CalCOFI cruises (Fig. 1, upper panel). The stock was probably less than 10,000 mt in the early 1970s. Currently, the spawning biomass may exceed 100,000 mt, which is still a small fraction of the maximum historic spawning biomass of 3.5 million tons. Some confusion exists regarding the timing of the recovery of the northern stock because FAO combines the landings for the northern and Gulf of California stocks. A new Mexican fishery on the Gulf of California sardine began in the early 70s, reaching a peak catch of over 300,000 tons by 1988 and has declined thereafter. The combined FAO landings give the impression that the northern stock underwent a striking recovery in the 70s and 80s coinciding with the striking recovery of the Japanese Stock (Kawasaki, 1991). The recovery of the northern sardine stock did not occur at the same time as the Japanese sardine; in fact, the northern stock did not exceed 20,000 mt until 1986 (Wolf, et al., 1987). Today (1993) the combined U.S. and Mexican catch of the northern sardine stock is about 60,000 mt. What was interpreted as a recovery was the development of a new Gulf of California fishery for sardine. Ironically, the Gulf of California stock, with catches declining since 1989, collapsed in 1993 with a total catch of less than 20,000 mt. It should be mentioned, however, that genetic analysis indicates that these stocks are part of a common population, but their dynamics are clearly different.

The current interpretation of the collapse of northern stock is that overfishing exacerbated a decline caused by environmental change, a decade of persistently cold sea water temperatures which were unfavorable to sardine recruitment. Recent work by Jacobson and MacCall (ms.) indicates that when sea surface temperatures (as measured at Scripps Pier) average 17.3°C the maximum sustainable yield (MSY) of sardine may be about five times the MSY when sea surface temperatures average 16.6°C. At this time the mechanisms responsible for the relation between sardine recruitment and sea temperature are unknown.

Smith, et al., 1992 estimated rates of California sardine population growth and decline using the scale deposition data from Baumgartner, et al., 1992 changes in standing crop of sardine eggs, and virtual population analysis. Fastest population growth was based on egg abundance of the northern stock of sardine (1975-1991) where annual growth was 70% per year, and fastest declines for the same population were 20-30% per year. Analysis of the effects of life stage specific differences in mortality and growth using Lefkovitch Matrix models indicate that population changes equivalent to those observed in sardine can be produced by altering early or late larval mortality or growth rates within the range of published values (Butler, et al., 1993). Thus, the central question for the California sardine from a climate change perspective is: what are the environmental conditions that persist over a decade or more, affect survival and growth of sardine larvae, and are correlated with three year average sea surface temperatures?

### 2.1.2 The Northern Anchovy (*Engraulis mordax*)

The northern anchovy population is divided into four stocks, a northern stock that extends from

British Columbia to San Francisco; a central stock which extends from San Francisco to Punta Baja, Mexico; and a southern stock that extends south from Punta Baja to Cabo San Lucas. In 1986 a recent invasion of northern anchovy into the Gulf of California (Mexico) was documented by Hammann (1989) indicating the formation of a new Gulf stock of anchovy. Sedimentary scale evidence indicates anchovy have not been in the Gulf for over 100 years (Baumgartner, pers. comm.). The recent invasion is in rough correlation with a decline in the Gulf sardine stock.

The largest and best known stock is the Central sub-population. The biomass of this stock was low in the 1950's and 60's (200-500,000 mt) grew rapidly in the early 70's, reaching a maximum historic biomass of 1.2 million tons in 1973 (Jacobson and Lo, 1993), and declined thereafter. Over the last 5 years the biomass has stabilized in the 300-400,000 mt range. A 60,000-300,000 mt reduction fishery existed from 1969 through 1989, but landings have been less than 11,000 mt since 1989. Declines in biomass in recent years were probably due to low recruitment rather than high fishing mortalities (Jacobson and Lo, pers. comm.). The most striking feature of the 30 year anchovy time series was an extra-ordinarily large recruitment in 1972, ushering in a decade in which 7 years exceeded the mean. This period of high anchovy abundance coincided with the continuing decline of the sardine.

A pair of clupeoids, a sardine and anchovy, exist as part of the pelagic fish assemblages in many of the worlds oceans. The decline in one member of the pair, usually the sardine, has occurred in rough correlation with an increase in the biomass of the other (Blaxter and Hunter, 1982). This has led to considerable speculation regarding the potential interaction of these two species. Since their food overlap is broad, inter-specific competition for food has often been inferred. The only direct evidence of interaction is provided by Butler (1991). He found that mortality rates of sardine larvae (>20d) increased between 1951-1967 and the increase was positively correlated with the increase in biomass of the northern anchovy. He attributed the correlation to predation by anchovy on sardine eggs and larvae.

Life stage sensitivity analysis for anchovy using Lefkovitch Matrix models indicates that the most sensitive stages were the early larval (4-10 mm) where the fastest growth rate or lowest mortality rate leads to a 270% increase in population size (Butler et al., 1993).

### 2.1.3 Pacific Mackerel (*Scomber japonicus*)

Two major peaks in the biomass of Pacific mackerel have occurred over historical times, 1925-1935 when the stock exceeded 400 thousand mt and during the early 80's when the stock reached the same level (MacCall, et al., 1985). The paleo-sedimentary record of Pacific mackerel scales indicates the 1925-35 peak and another one around 1830. Thus, three major outbreaks of Pacific mackerel have occurred over the last 162 years. The 1925-35 and 1980s peaks coincided with warm water regimes. Minimum levels of abundance occurred in the late 60s reaching less than 10,000 mt by 1966, and remaining low until the late 70s. The 1976 year class that initiated the recovery of the fishery was in the upper 25% of all year classes, but it was produced by a spawning biomass of less than 10,000 tons. The stock has been declining slowly since the peak biomass in 1982; the estimated 1992 biomass was 124,000 mt.

Unlike sardine and anchovy, no dependable data exists on egg and larval mortality rates nor on larval and juvenile growth in the sea. Accurate estimates of larval mortality may never be practical because of the highly patchy distribution of the spawn. Preliminary work indicates that some mackerel females spawn daily (Dickerson, et al., 1992) but estimates of stock spawning rates would be difficult and costly due to the patchiness in the distribution of spawning and non-spawning fish. For these reasons either anchovy or sardine may be preferable to mackerel as a subject for cooperative research on effects of Climate Change on fish population dynamics.

### 2.1.4 Pacific Herring (*Clupea pallasi*) of the Northeastern Pacific Ocean

#### Distribution & Biology

In the Northeast Pacific herring are distributed along the west coast of North America from California to the Chuckchi Sea with some small stocks in estuarine arctic waters. The greatest abundance is from British Columbia to the Bering Sea. Stocks in California, Oregon, and Washington are small relative to the more northern stocks. Major aggregates of stocks are harvested in San Francisco Bay, Northern Washington-Southeastern Alaska, Prince William Sound, Kodiak Island, Cook Inlet, and eastern Bering Sea in North America.

Pacific herring spawn exclusively in spring, in shallow inter- and subtidal waters. After a 2-3 week incubation, eggs hatch into pelagic larvae and disperse throughout local nearshore coastal waters. After a 1-2 month larval stage the young herring reside mainly in nearshore waters for a 1-2 year juvenile period. They mature sexually in 2-4 years (earlier in south) and spawn once per year for the remainder of their lives. Most herring live for 4-5 years with a few living to 15 years (Grosse & Hay, 1988).

Adults spend summers in a relatively large number of small, dispersed schools and feed mainly on copepods and euphausiids. Movement to summer feeding grounds for larger stocks may require extensive migrations of several hundred kilometers or more, to offshore banks, while migrations to feeding grounds of smaller stocks may be more geographically restricted. In the winter, adult herring form a small number of large aggregations in the same overwintering areas each year. In the spring herring move from these areas to spawning areas, that also are consistently occupied each year.

#### Stocks and fisheries

North American herring fisheries started as food fisheries in the early 1900s producing salt or dried herring. In the late 1920s industrial herring fisheries developed for oil and meal and catches rose rapidly in British Columbia to South-central Alaska where the largest fisheries occurred. Reduction fisheries persisted until the mid-1960s when the fishery closed due to economic competition from Peruvian anchovy and other cheaper meals, and the closure of some fishing areas to preserve herring for salmon forage. In British Columbia a moratorium on herring fishing was established, following a collapse of the herring stock in the mid-1960s (Fig. 2), and maintained until stocks recovered in the early 1970s (Hourston, 1980).

In the absence of fishing, the British Columbia stocks began to increase and in 1972 a roe fishery began which grew to a peak harvest of 80,000 t in 1976-78. In subsequent years the harvest was reduced to about 30-40,000 mt because of concern that high harvests could not be sustained.

Roe herring fisheries also developed in Alaska in the early 1970s, and harvests have been very conservative with exploitation at 10-20% of estimated biomass which has averaged less than 10,000 t annually. In the eastern Bering Sea a distant water fishery was established in the late 1950s by Russian and Japanese vessels. Catches rose rapidly to a peak in the early 1970s, and then declined, and the off-shore foreign fishery was replaced by an inshore roe herring fishery in the late 1970s.

Individual stocks of herring in the northeastern Pacific Ocean have exhibited wide variations in abundance. Sometimes, exceptionally large year classes, such as one in 1977, were synchronous over broad geographical ranges (from Vancouver Island to central Alaska). In other years there may be large differences in cohort strength between reinforcing stocks, such as the Queen Charlotte Island and the mainland of British Columbia. Year-class synchrony in the northeastern Pacific appears to correspond to hydrographic domains with distinctly different recruitment patterns between Alaskan and Canadian stocks (Zebdi and Collie, ms).

In the eastern Bering Sea only about a third of the variation in year class strength can be accounted for by variation in spawning stock size, indicating that environmental factors are important determinants of year-class size (Wespestad and Gunderson, 1991). Climatic effects of wind-driven transport and temperature describe a portion of the residual variation in recruitment, but about 50% of the total variation is left unaccounted. The remaining variation may relate to large-scale physical processes, or local variation in biological processes, for which accurate measures are unavailable.

In the middle part of their range, Washington to central Alaska (Prince William Sound) herring are the most abundant small coastal pelagic fish. They are consumed as principal or secondary prey by many piscivores such as the Pacific cod (*Gadus macrocephalus*), the chinook and coho salmon (*Oncorhynchus tshawytscha* and *O. kisutch*), Pacific hake (*Merluccius productus*), as well as many sea birds and marine mammals (Hay et al., 1992). In this capacity they serve as a principal vehicle for energy transfer from lower to higher trophic levels. Predation has been shown to be a significant source of mortality and may contribute to variation in year-class size (Walters, et al., 1986; Ware 1991). Predation on herring is modified by environment in some cases. Ware and McFarlane (1989) found that in El Niño years hake extended their range into areas occupied by herring resulting in increased herring mortality.

## 2.2 Western Pacific

### 2.2.1 Japanese Sardine (*Sardinops melanostictus*)

A major part of this section is based on preliminary results of the BICOCOSMOS project, a ten year research project on Japanese sardine ecology and population dynamics, which began in 1989; results from this project will appear in journals in the near future.

Isozyme analysis for genetic divergence indicates that several stocks of Japanese sardine (*Sardinops melanostictus*) are a single population. The population fluctuated greatly over the last two decades; it began to increase in the mid-70's, reached a peak in the mid-80s, and has been declining since 1989. Total catch of the Japanese sardine was 20,000 mt in 1970. It increased to 2,210,000 mt in 1980 and reached a maximum of 4,490,000 mt in 1988. The catch declined after 1989, falling to about 2,000,000 mt by 1992.

On the Pacific side of Japan, sardine spawn along the Kuroshio Current in February and March. Eggs hatch two days after fertilization at 17-18°C and the larvae start feeding within two days after hatching. Egg and larvae are transported to the east by the Kuroshio Current as fast as 2-3 knots (1.0-1.5 m/sec) and in a few months when the larvae are 20-30 mm, they reach the Kuroshio Extension off the Boso Peninsula east of Honshu Island, Japan. Part of the cohort leaves the Kuroshio Current and enters the coastal waters along the Pacific side of Honshu Island forming shirasu fishing ground for sardine larvae.

While being transported by the Kuroshio Extension, the larvae metamorphose into the juvenile stage and in early summer they start a northward migration through the mixing water between the Kuroshio and the Oyashio fronts. They use warm streams and warm core rings derived from the Kuroshio Extension as migratory paths. They cross the Oyashio front and feed on abundant zooplankton and phytoplankton in the Oyashio water in summer. In autumn they migrate south to the waters off Boso Peninsula. The one year old sardines return to Oyashio waters the following summer.

The sardine mature in 2 or 3 years. Short day length and a decrease in water temperature in autumn induces sexual maturation and southward migration to the spawning grounds. Nutritional conditions of females at the beginning of sexual maturation have a major effect on the reproductive effort during the subsequent spawning season (Tsuruta, 1985). Batch fecundity varies from 20,000-40,000 eggs depending on nutritional condition (fat reserves) of females, but the number of batches spawned by females per season is not known). Eggs from fat females are of good quality having a larger yolk volume and higher content of polyunsaturated fatty acids than those from thin females (Morimoto, 1991).

Since 1990 the percentage of the number of landed sardines older than 4 years has increased rapidly (Fig. 3). The percentage was about 30% or less in the years before 1989, but in 1991 and 1992 it increased to more than 90%.

The number of 1 year old sardine caught in waters east of Hokkaido Island is used as a recruitment index in Japan. From 1986 to 1988 the number of recruits ranged from 2,000-5,500 million fish, but decreased to 0-600 million in 1989-1992. Thus, the population has decreased since 1988 because of recruitment failure. Average egg production in the Pacific side of Japan in 1989-1992 was 4,600 trillion. The recruitment failure was assumed to be due to low survival rates in the stages between the egg to juvenile stage.

When the population was in the early phases of growth in the mid 1970's, the recruitment index (mentioned above) was stable as it ranged between, 1,500-2,000 million fish. When the population was in the older growth phase, reaching a peak biomass 1979-1987, the recruitment index was much more variable ranging between 32 million to 5.9 billion fish with a dominant year class occurring every three or four years. The recruitment failed in four successive years after 1988. In summary, three patterns in recruitment were evident during the rise and current fall of the population. Stable recruitment associated with a growing population, fluctuating recruitment associated with sustained high biomass, and recruitment failure associated with population decline. The population growth and decline of the sardine over the last two decades is considered to be caused by a variation of recruitment which might be due to changes in the mortality of early life stages.

### 2.2.2 Japanese Anchovy (*Engraulis japonicus*)

The Japanese anchovy population is divided into four stocks which occur in the following four localities: northern Pacific, southern Pacific including Seto Inland Sea, East China Sea, and Japan Sea. Annual landings were high (350-450,000 mt) in 1950s and 1960s when the Japanese sardine (*Sardinops melanostictus*) population was very low, but landings decreased rapidly after 1975, as the sardine population increased. In the 1980s, the landings remained at a low level (150-200,000 mt). The landings have recovered since 1989 as the sardine began to decline. However, the maximum anchovy catch is only a tenth of that of the sardine, and the stock fluctuations are relatively moderate (see Table 2).

The north Pacific stock of anchovy is the largest and most studied. The spawning habits and demography of the stock change with population size, (Funakoshi, 1987). When the stock is small, almost all spawn at one year old in coastal waters and bays during summer and autumn and die after spawning. Their migration range is restricted to the spawning ground areas. On the other hand, when the stock is large they mature at one year old and spawn in coastal and offshore waters in spring. A large proportion survive after spawning and spawn again in next spring. Their migration range extends to the waters off southern Hokkaido.

Watanabe (1992) mentioned that the stock-recruitment relationship based on the total number of eggs spawned seemed to fluctuate clockwise around a certain equilibrium stock level. Funakoshi (1990) concluded that anchovy in plankton rich coastal waters have a higher fecundity, and spawned more frequently, than those spawning in offshore areas where food was less abundant. Laboratory experiments indicate that when food is reduced, anchovy spawn less frequently and the interval between spawning increases. The number of eggs spawned per female was reduced at high fish density even when food was held constant indicating density dependent affects on egg production (Tsuruta and Hirose, 1989).

A common belief is that anchovy populations vary inversely with sardine populations, but the long-term landing data of pelagic fishes in Japan seem to indicate a more complex pattern of interactions among pelagic species. These data indicate the following sequence: chub and spotted mackerels (*Scomber japonicus* and *Scomber tapaeinocephalus*, group A) was replaced by the sardine (species B); the sardine was replaced by a group of four species (group C), the anchovy (*Engraulis japonicus*), Pacific saury (*Cololabis saira*), and jack mackerels (*Trachurus japonica* and *Decapterus muroadsi*); and the four species in group C were replaced by the mackerel (Fig. 3). Matsuda, et al. (1991, 1992) proposed an inter-specific competition model for groups A, B, and C as a hypothesis for the species replacement. If species A causes a decline in the population of B, B causes a decline in C; and C causes a decline in A, the model predicts that the abundance of these three groups fluctuate forever and dominate in cyclic order. The kinds of interactions occurring among these three groups are not well understood, however. Improved understanding of their interactions seems to be an essential prerequisite for understanding the dynamics of these populations.

### 2.2.3 Japanese Common Mackerel (*Scomber japonicus*)

Two mackerel species are fished commercially around Japan, the common mackerel and the spotted mackerel (*Scomber japonicus* and *Scomber tapaeinocephalus*). The Japanese common mackerel is a widely distributed migratory fish, while the spotted mackerel has a much smaller range occurring principally in the southern part of Japan. The range for the common mackerel is even wider than that of the Japanese sardine. The northern limits to their distribution is about the same, but unlike the sardine, the common mackerel occurs in the East China Sea (recent catch is 110,000-250,000 mt).

The range of surface temperature for fishing common mackerel falls between 14-18°C. When the stock is large, common mackerel make large scale north-south migrations. The migration to the north is a feeding migration, while the southern migration is a wintering and spawning migration, similar to the sardine. The common mackerel population around Japan consists of four local stocks: Pacific; South Pacific; East China Sea; and Tushima Current (Japan Sea).

In recent years, the landings of the Pacific stock are 60-70% of the total Japanese landings. The catch from the Pacific stock increased remarkably in the 1970's reaching a peak of 1,300,000 mt in 1978; recent catches fluctuate between 200,000-300,000 mt.

### 2.2.4 Pacific Saury (*Cololabis saira*)

Pacific saury occurs throughout most of the northern Pacific. In the Western Pacific, saury is one of the major commercial species taken by Japanese, Russian, and Korean fisheries. No estimation of the population size exists because the distribution of the larvae, juveniles and adults is continuous from the Western to the Eastern Pacific.

After World War II, a new fishing gear, the stitch-held dipnet (bouke-ami), was introduced in Japan. Total catch increased remarkably after the introduction and reached a peak during 1955-63 with a maximum catch of 575,000 mt in 1958. Catch decreased in late 60s down to 52,000 mt in 1969. Annual fluctuation of the catch was quite large in 70s ranging between 87,000 to 427,000 mt. In the 80's, the catch stabilized because of landing regulations adopted by the saury fishermen association. Abundances of larvae, juveniles, and adults indicate that the population in the Western Pacific has been increasing since 1988.

Saury spawns off the northern Honshu Islands in autumn and spring, and in the Kuroshio area in winter. Juveniles from different spawning seasons start migrating north in early summer to the Oyashio area where they feed on abundant zooplankton, especially *Neocalanus plumchrus* and euphausiids. Otolith analyses (Watanabe, 1988), rearing experiments (Hotta, 1958, Watanabe and Kuji, 1991), and increase in body length of northward migrating groups (Fukushima, et al., 1990), all indicate that the Western Pacific saury reaches a length of 30 cm in one year. Three length modes occur in fish caught in fishing season from late August to early December. The large fish are assumed to originate from eggs spawned in the autumn, the medium sized fish from winter eggs and small fish from spring spawnings (Fukushima, et al., 1990). The three groups are not thought to be from different stocks because the genetic distances of size groups are too close to be regarded as separate stocks.

Size composition of landed sauries differs annually, and differences in size composition affect price and the total weight of the catch. The length composition of the catch is believed to be related to relative recruitment of autumn, winter and spring spawning cohorts. Pre-season forecasts of size composition of the catch is of great value to fishermen and fish processors. The Tohoku National Fisheries Research Institute provides forecasts of recruitment based on three parameters: larval production at hatching, growth and mortality rates in larval and juvenile stages. Using these parameters, they estimate daily production of 50 mm juvenile for autumn, winter and spring spawnings. Rearing studies indicate that by the time saury juveniles reach 50 mm and begin schooling, they have passed through the high mortality period.

### 2.2.5 Yellow Sea Herring (*Clupea pallasi*)

The Pacific herring in the Yellow Sea, which is traditionally called Yellow Sea Herring, has a long history of exploitation. The importance of herring is demonstrated by the existence of villages and localities named for their association with it. In this century, the commercial fishery has experienced two peaks (in about 1900 and 1938) followed by a period of little or no catch. In 1967, due to the recovery of the stock, a large number of 1-year old herring began appearing in bottom trawl catches. The catch increased rapidly to a peak of 200,000 mt in 1972. The high catches were due to the very strong 1970 year class and reached a historic maximum abundance estimate of 26.8 X $10^8$ fish (at age 1). Since 1982, the stock has declined apparently due to the occurrence of a series of weak year classes. The catch has declined to below 1,000 mt in 1989-1990.

Obviously, Yellow Sea herring have been characterized by strong fluctuations in abundance. Tang (1981 and 1987) found that there is no strong relationship between spawning stock and recruitment and that environmental conditions such as rainfall, wind, and daylight are the primary causes of fluctuations in recruitment. Long-term changes in biomass may be correlated with the 36 year cycle of dryness/wetness oscillation in eastern China.

## 3.0 SCIENTIFIC QUESTIONS AND HYPOTHESES

The Working Group discussed the scientific questions and hypotheses required for an understanding the causes of variability of pelagic fish populations. Four key questions and their associated hypotheses are discussed briefly below.

**3.1 What differences exist among Pan-Pacific pelagic stocks in biomass and stage specific vital rates?** Implicit in this question, is the hypothesis that stage specific vital rates determine the variability of fish populations and density dependent processes play a subsidiary role. Pan-Pacific comparisons of vital rates might help answer the questions: 1) why does the western Pacific boundary system support a higher biomass of small pelagic fishes than does the eastern Pacific boundary system? and 2, Why do pelagic fishes show different fluctuation patterns in the same region? The group concluded that detailed descriptions and comparisons of fish biomass and stage specific vital rates, such as growth, mortality and fecundity are the first step in understanding the mechanisms underlying population fluctuations of small pelagic fishes.

**3.2 How does physical forcing affect population processes?** Implicit in this question is the hypothesis that variability in population size is determined largely by density-independent factors such as changes in regional oceanographic conditions. A further extension of this hypothesis is that a Pan-Pacific ocean climate influence on fish population dynamics exists and that regional comparisons are necessary to identify the details and modes of actions. Regional comparisons of similar species could lead to identification of the similarities in oceanographic conditions that correspond to population growth or failure, regardless of the validity of the Pan-Pacific hypotheses.

**3.3 How do biomass specific changes in life history traits, such as expansion and retraction of spawning habitats or latitudinal extent of feeding migrations, affect population variability?** Implicit in this question is the hypothesis that density-dependent processes play a major role in population growth. In coastal pelagic fishes important population traits seem to vary with population size, including: growth; age or size at maturity; spawning habitat selection; and the tendency to migrate. At high biomass levels, populations may have large migrations, slow growth, and older age at maturity with the opposite pattern at low biomass levels. A more specific hypothesis underlying this question is that density-dependent habitat selection affects reproductive success and population growth through the physical properties of the habitats selected.

**3.4 How do the interactions between populations of small pelagic fishes affect their populations?** No doubt exists that coastal populations of sardine, anchovy, and mackerel interact. As they all are pelagic planktivorus, their diets broadly overlap and they may consume each others egg or larval stages. In addition, large mackerel may prey upon adult anchovy and sardine as well as their early life stages. Thus, population interactions should affect the productivity and growth of pelagic fishes in the coastal ecosystem. The tacit assumption underlying this question is that species interactions play a role in population variability and shifts in dominance among pelagic fish.

## 4.0 CRITICAL GAPS IN INFORMATION AND KNOWLEDGE

A major challenge for marine science in the twenty-first century will be to forecast how long-term changes in ocean climate will affect our natural marine resources. The obvious first step is to explain past fluctuations in the abundance of stocks. Unfortunately, we lack the information, and the basic level of understanding necessary for a documented and coherent ecological explanation for the history of population growth and decline of North Pacific pelagic fishes. We do not know how physical forcing increased the survival of eggs or larvae to produce the great year classes of the past, nor do we understand the role played by population size and pelagic species interactions in the formation of those year classes. No shortage of plausible mechanisms exists and some have been validated by direct field measurement, but we lack the information needed to test these mechanisms analytically, and we lack the understanding necessary for a synthesis of physical forcing and density dependent mechanisms that would explain stock histories as we have observed them. We believe that the comparative studies we propose will help fill these gaps in understanding.

Initial requirements for a north Pan-Pacific investigation of climate effects on the dynamics of fish stocks are that estimates of abundance, recruitment, and vital population rates are available and that a strong Pan-Pacific communication network exists. Neither of these initial requirements are presently met. We lack data on some of the vital rates of even the best studied stocks, existing data on rates and population statistics are not generally available on a Pan-Pacific basis, and no adequate communication system exists for the development of Pan-Pacific comparative studies.

# 5.0 POSSIBLE SCIENTIFIC APPROACHES

The group identified various ways critical gaps in data understanding and communication might be filled and key scientific questions might be resolved. All approaches considered by the group are included.

## 5.1 Assembly of Data

The group placed a high priority on the assembly of time series of available data on annual biomass and recruitment levels, and on stage-specific vital rates for the key pelagic stocks. Such information may include: annual biomass, recruitment and catch; sex, first maturity and fecundity by length or age; spawning habitat characteristics such as temperature and season; egg incubation rates and mortality; and larval and juvenile mortality and growth.

This initial assembly of biological data should be followed by an assembly of time series of relevant oceanographic data for the areas occupied by the stocks. Relevant oceanographic indices could be selected for each area from results of detailed process studies, or by using forcing functions proposed in the literature. Biological data on zooplankton abundance, and the food habits of coastal pelagic fishes would also be desirable.

If fishery data, or data on specific vital rates, are missing for key populations, these data gaps could be filled by a directed program to collect and process such data.

## 5.2 Expansion of Scientific Knowledge

### 5.2.1 Pan-Pacific Comparisons of Recruitment

Exploratory comparative time series analyses of the biomass and recruitment for key coastal pelagic stocks need to be conducted to determine common patterns in stock fluctuations (using approaches similar to Hollowed et al., 1987). These analyses would be most fruitful if they focused on East-West (e.g. California sardine and Japanese sardine) and North-South (e.g. herring) comparisons. The next step may be to couple oceanographic data and models to the fishery analyses, to evaluate hypotheses concerning physical forcing of coastal pelagic stock fluctuations. For example, do similar oceanographic conditions and processes produce similar responses among different coastal pelagic fishes? Fish stock distributions and vital rates could be examined relative to latitude and longitude, seasonal temperature, and current patterns. Analyses of other aspects of the system (e.g. primary or secondary productivity) may also provide information for estimating upper or lower limits of fish production.

Inclusion of all possible spawning groups in Pan-Pacific comparisons, would greatly increase the richness of the comparison. Herring, sardine, and anchovy form a mosaic of habitat specific spawning groups, each with unique population dynamics and life table characteristics. Pacific herring are particularly prolific in this regard, with spawning groups associated with specific small intertidal areas, while spawning groups of sardine and anchovy are larger and more regional in character. Comparisons between these groups are useful because they reflect regional habitat differences, even though modern genetic studies often fail to find differences between them. For example, although genetic studies indicate that the sardine population around Japan belongs to one stock, a group of sardines spawn west of Kyushu Island and migrate into the Sea of Japan where oceanographic conditions are considerably different from the Pacific side. One would expect spawning and recruitment and vital rates to differ between the Japanese Sea and Pacific spawning groups.

Recruitment comparisons should not only consider single years of great recruitment success or failure, but should also consider successions of stronger than average year classes, or periods when year classes consistently failed. It is important to consider in such an analysis not only the environmental conditions that correlate with these periods, but also the affect of such successions of strong or weak year classes on population growth and stability. A number of strong year classes may stabilize the population while a small number of weak year classes may make the population more susceptible to environmental variability.

### 5.2.2 Life Table Analysis

Life stage matrix models, such as the Lefkovitch model (Lefkovitch, 1965; Caswell, 1989), provide a useful way to begin comparative work. First, they require an inventory of life table data and thereby identify critical gaps in knowledge. Second, they help assess the quality of the information by tests of population stability. Third, they permit assessment of the sensitivity of the population to changes in rates within each life stage. Lastly, they provide a simple standardized way to evaluate effects of physical forcing on population growth. For these reasons, completing a Lefkovitch matrix for each species to be compared would be a useful first step in the development of a PICES comparative study.

An important and recent refinement of life stage matrix models for fishes is to include variance as well as mean duration of stage and mortality (Lo, et al.; ms.). This approach adds new information, and the costs are low because the durations of early life history stages can be obtained from daily growth increment analysis of juveniles (Butler, 1989 and 1991). When variances are included the modeled population is generally less sensitive to changes in vital rates than when only the mean is used, and the results are probably more realistic.

### 5.2.3 Trophic Ecology

To examine the overall functioning of Pan-Pacific ecosystems an inter-regional comparison of the gross production and biomass at several trophic levels (primary and secondary levels, and small pelagic fishes) would be useful. This would provide a preliminary idea of the overall functioning of Pan-Pacific ecosystems and might help explain the differences in fish production between systems. A more thorough treatment of trophic relations using trophodynamics modeling is also strongly recommended. Trophodynamics modeling is defined as modeling of the food web linkages that support the production of key pelagic fish species. By trophodynamics modeling, the response of marine production systems to environmental changes can be analyzed, based on the flows and balance of biomass among the trophic levels. This technique will be useful for understanding the biological processes which control population fluctuations and species interactions. Model construction can also reveal the lack of knowledge on relationships among biological components and physical forcing functions. Once the model can generate the average annual cycle of fish production, various hypotheses on the relationships between environmental change and population fluctuations can be examined. This approach becomes more powerful when such models are constructed for several different regions with ecologically similar species.

### 5.2.4 Comparative Field and Laboratory Studies

The focus of most of the Working Group's discussions were on the analysis of existing data because such work is an appropriate starting point. The Group recognized in the long term, Pan-Pacific field and laboratory work using standardized methods and approaches would have great benefits. One approach might be to focus the field work on accurate interannual measurements of age specific fecundity and life stage specific growth or stage duration and their links to physical forcing. These fish population parameters are among the least expensive to measure, yet they might reveal substantial differences between populations and ecosystems. In contrast, mortality is an expensive parameter to measure directly by sampling larvae and juveniles requiring many more samples and days at sea. In addition, using modern otolith reading systems one can digitize long chronologies of daily growth records from a single otolith. When such data from a number of juveniles are combined, estimates of mean growth and variance for many life stages can be provided.

It also may be useful to collect larvae from stocks with different growth rates and rear them under identical conditions to determine if such growth rates are genetically or environmentally determined.

## 5.3 Sharing Knowledge and Technology

PICES has the opportunity for leadership in the Pan-Pacific exchange of knowledge among marine researchers. Presentations at PICES Annual meetings and workshops are important ways that PICES has opened the avenue of communication by providing a forum for exchange of ideas. In addition to these approaches, the working group considered several other ways to improve Pan-Pacific communication.

All members believed that informal scientific communication and possible collaboration would increase if a directory of key Pan-Pacific researchers were available. The Working Group proposed to compile a list of key researchers who study coastal pelagic fishes of the North Pacific within their respective geographic regions. The directory, would include not only agency or institution, address and FAX, but would include pertinent information such as species of interest, key-words describing broad topics of interest and areas of present research. This final compilation of researchers in all member countries should be made available in a paper copy and also maintained on a computer data base which should be updated annually.

Another way PICES could foster communication and build collaborative efforts is through Pan-Pacific exchange of the researchers. The Group believes that of all the activities sponsored by PICES, few could have as great and immediate benefit as a PICES visiting scientist program. The Group recommended that the Secretariat develop a PICES visiting scientist exchange program. Such a program might provide 2-4 visiting fellowships per year to the PICES community with a duration of a month or more. Selection of applicants would be competitive based on a short letter of intent, CV, and references. Applicants would include agency as well as academic scientists and funding would cover only travel and subsistence costs. If PICES does not have sufficient funds to support the program, some working Group members would be willing to work with the Secretariat to find outside funding. It would be preferable if the Secretariat managed the funds to minimize indirect costs.

# 6.0 TABLES AND FIGURES

Table 1. Catch statistics of small pelagic fishes in 1990.

| SPECIES | | CATCH IN THOUSAND TONS | |
|---|---|---|---|
| **Common** | **Scientific** | **World** | **North Pacific** |
| Atlantic herring | Clupea harengus | 1,538 | *** |
| Pacific herring | Clupea pallasi | 199 | 199 |
| Japanese sardine | Sardinops melanostictus | 4,735 | 4,735 |
| South American pilchard | Sardinops sagax | 4,254 | *** |
| European pilchard | Sardina pilchardus | 1,540 | *** |
| California sardine | Sardinops sagax | 399 | 399 |
| Anchoveta | Engraulis ringens | 3,772 | *** |
| European anchovy | Engraulis encrasicolus | 539 | *** |
| Japanese anchovy | Engraulis japonicus | 442 | 442 |
| South African anchovy | Engraulis capensis | 201 | *** |
| Northern anchovy | Engraulis mordax | 6 | 6 |
| Japanese common mackerel | Scomber japonicus | 1,391 | 751 |
| Atlantic mackerel | Scomber scombrus | 657 | *** |
| Chilean jack mackerel | Trachurus murphyi | 3,828 | *** |
| Atlantic horse mackerel | Trachurus trachurus | 420 | *** |
| Cape horse mackerel | Trachurus capensis | 346 | *** |
| Japanese jack mackerel | Trachurus japonicus | 250 | 250 |
| Pacific saury | Cololabis saira | 416 | 416 |
| **Small Pelagics Total** | | **24,933** | **7,198** |
| **Marine Fishes Total** | | **70,666** | *** |

Source: FAO Yearbook of Fishery Statistics

Table 2. Comparison of the catch or biomass variability of small pelagic fishes from Japan and California.

| CHARACTERISTICS OF PELAGIC FISH CATCH OR BIOMASS DATA (Thousands of Tons) | JAPANESE STOCKS[a] | | | | CALIFORNIA STOCKS | | |
|---|---|---|---|---|---|---|---|
| | Sardine | Anchovy | Mackerel | Saury | Sardine | Anchovy | Mackerel |
| | Catch | Catch | Catch | Catch | Biomass[b] | Spawning Biomass[c] | Biomass[d] |
| Years data available | 1957-87 | 1957-87 | 1957-87 | 1957-87 | 1935-90 | 1954-91 | 1929-91 |
| Mean | 878.3 | 300.7 | 778.1 | 274.8 | 619. | 413. | 143. |
| Maximum | 4179.4 | 430.2 | 1625.9 | 575.1 | 3628. | 817. | 440. |
| Minimum | 9.2 | 134.6 | 234.8 | 63.3 | <20.[f] | 131. | <20.[f] |
| Max./Min. | 454.3 | 3.2 | 6.9 | 9.1 | 62.4 | 6.2 | 22. |
| Coef. Var. % | 150. | 30. | 50. | 50. | 181. | 69. | 92. |

a. Funakoshi, 1990
b. Jacobson and MacCall ms., 1993
c. Jacobson and Lo, 1993
d. Jacobson unpublished data
f. Biomass uncertain but below 20,000 tons

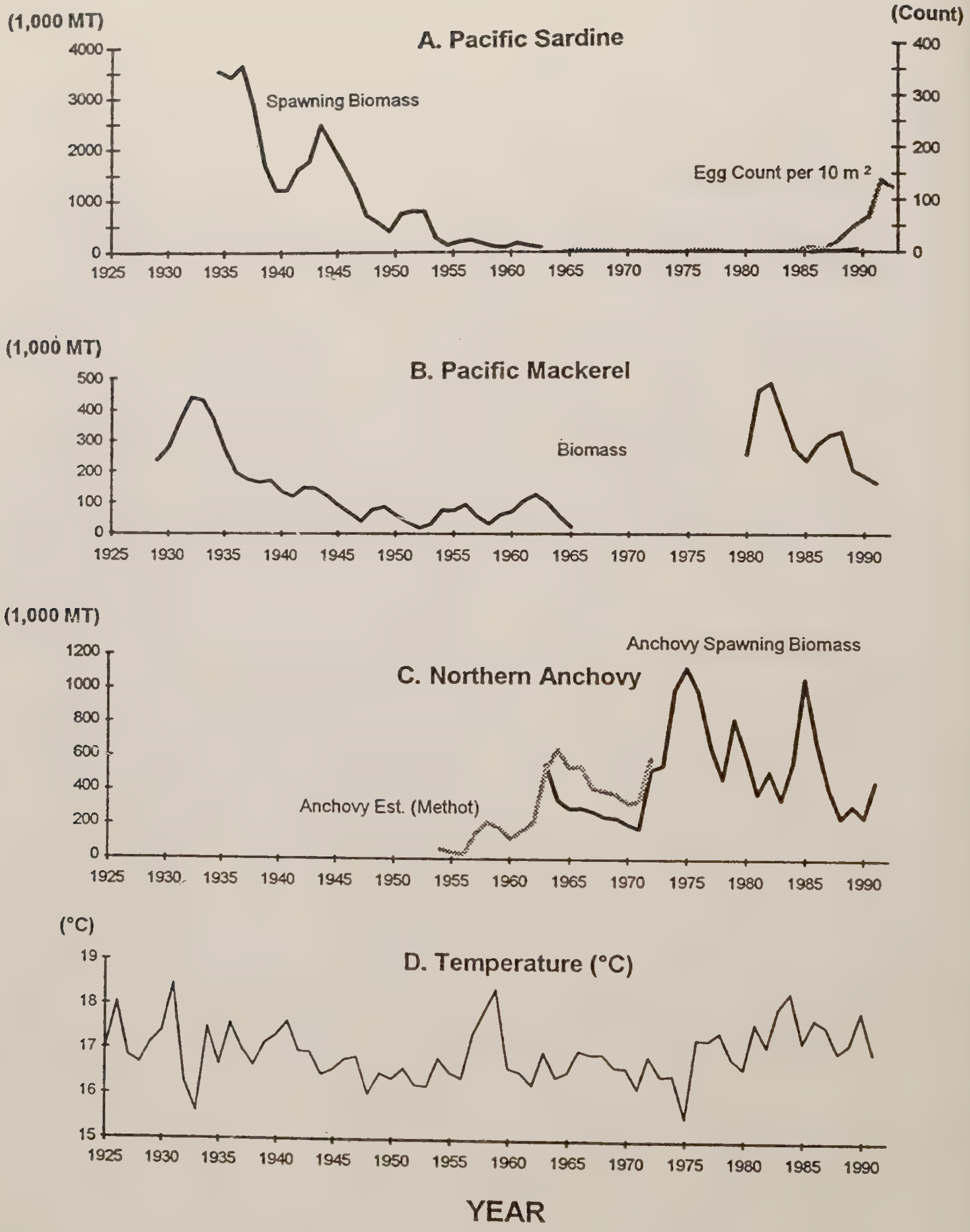

Fig. 1. Time series of estimates of the biomass of California coastal pelagic fishes and the average water temperature taken at Scripps Pier (La Jolla, California).

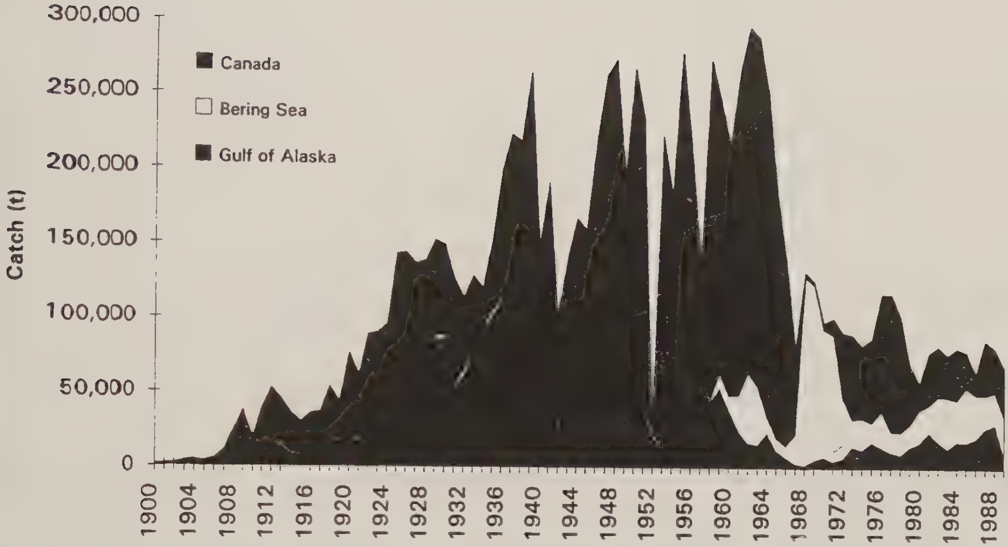

Fig. 2. Catch of herring off Canada, Gulf of Alaska, and in the eastern Bering Sea, 1900-1990.

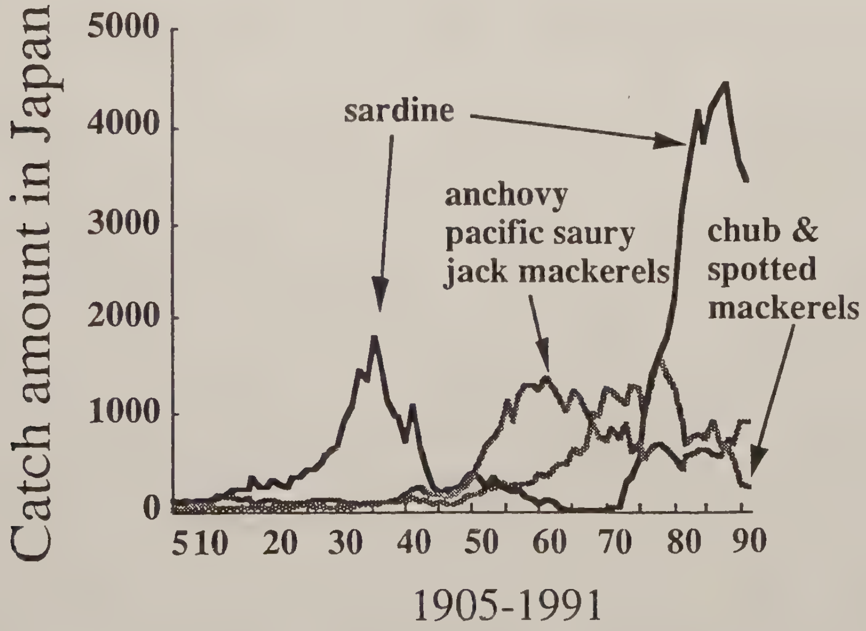

Fig. 3. The long-term fluctuation of annual catch of several species of pelagic fishes combining three groups: Japanese sardine; Japanese anchovy, Pacific saury, and jack mackerels; chub and spotted mackerels in 1905 to 1991 (after Matsuda et al., 1992).

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# 8.0 Appendices

## Appendix 1

### Recommendations and Actions

#### Science

* Assemble information on Western and Eastern Pacific Coastal pelagic fish populations. Fishery information shall include: stock size, catch, and recruitment estimates per year. Also, life table data containing life stage specific rates of growth, mortality and reproduction shall be required. PICES Working Group 3 agrees to produce a document containing these data for key coastal pelagic species of the Eastern and Western Pacific. The document shall be completed in time for PICES Working Group meeting in 1994.

* Encourage the inclusion of Russian and Korean fish population information data on herring and other northern coastal pelagic species in the data exchange described in item 1.

* Encourage development of relevant oceanographic time series to facilitate the interpretation of Pan-Pacific patterns in recruitment success.

* Apply trophodynamics models in Eastern and Western Pacific ecosystems to understand how the production systems of each region support pelagic fish biomass. This work may require inclusion of pollock and hake.

* In the annual 1994 PICES meeting Working Group 3 shall review the fish population document described in item 1 and establish plans to carry out Pan-Pacific comparisons of life table differences and recruitment.

#### Communication

* Members of Working Group 3 shall make an inventory of scientists working on key coastal pelagic fishes within their respective geographic area. Working Group 3 will compile a list of key persons, addresses and topics of study and make it available to all interested researchers.

* The PICES COASTAL PELAGIC FISH WORKING GROUP requests PICES Fishery Committee to seek support of the PICES Secretariat in obtaining funds for a visiting scientists program. The working group feels that working visits of PICES scientists to other PICES countries is essential. Recognizing that PICES may not have funds to directly support such an action, the working group stands ready to assist the Secretariat in preparation of proposals to foundations and agencies to support the visiting PICES scientist program.

#### Administration

* The proposed inventory of fishery time series data and life table information along with the PICES Nemuro Workshop Reports will constitute important working documents for PICES. Such documents need to be organized and archived in some consistent way. For that reason, we recommend to the Fishery Committee of PICES that the Secretariat establish an informal administrative report series. The minimum requirements for such a series are: each working document is assigned a unique administrative report number; a standard cover design is used on each

copy of the report; a standard citation for the reports be established; report date; report number, and names of editors are clearly indicated. To reduce PICES costs, actual production of the report could be assigned to chairpersons, with a certain number of copies to the Secretariat. Of course, a more formal system could be adopted as well.

- Working Group 3 recommends continuation of the Working Group under the existing terms of reference but also recommends a name change to PICES COASTAL PELAGIC FISHES WORKING GROUP.

**Appendix 2**

### Terms of Reference

### Working Group 3
### Dynamics of Small Pelagics in Coastal Ecosystems (FIS)

- develop a program for a comparative study of the population dynamics and productivity of small pelagics (focusing on herring, sardine, anchovy and mackerel) in the coastal ecosystems along the western and eastern continental margins of the North Pacific;

- review the present state of knowledge, identify the key scientific questions and hypotheses that could be tested, including environmental effects on fish production and ecosystem structure;

- identify who is working in this field, and what data are available for retrospective analyses;

- determine which member countries would be willing to participate in a coastal ecosystems program.

**Appendix 3**

### List of participants

Working Group 3 members:

**Canada**
Dr. Douglas E. Hay
Dr. R. Ian Perry

**China**
Prof. Qi-Sheng Tang

**Japan**
Dr. Ichiro Hara
Dr. Yasunori Sakurai
Dr. Tokio Wada (Co-Chairman)
Dr. Yoshiro Watanabe

**U.S.A.**
Dr. John R. Hunter (Co-Chairman)
Prof. Brenda L. Norcross
Dr. Richard H. Parrish
Dr. Vidar G. Wespestad

Non-member:
Dr. Hideo Yoshida (Japan)

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# Bathymetric Demography and Management of Dover Sole

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*Abstract.*—Bathymetry is a key element in the demography of Dover sole *Microstomus pacificus*. Juvenile Dover soles begin life in relatively shallow water on the continental shelf but move gradually down the continental slope into deeper water as they grow and reach sexual maturity. Large and old individuals may eventually reach depths greater than 1,500 m. The ontogenetic migration of Dover soles into deeper water gives rise to a general pattern of increasing fish size with water depth, but there are differences between sexes and locations. To describe these patterns in greater detail, we computed probability distributions for depth, length, and sex using research trawl data for Dover sole taken off central California and Oregon. Our results indicate that females live at greater depths than do males and that abundance of large Dover soles may be lower at depths where lowest oxygen concentrations occur. In addition, major differences in bathymetric demography exist between study sites due, we suggest, to differences in bottom topography. We used one group of probability distributions and logbook data for Oregon and central California in a simple model to demonstrate how depth of fishing and bathymetric demography complicate interpretation of length composition and other data from a commercial fishery. Results from the model indicate that depth-stratified assessment models may be required to interpret fisheries data for Dover sole and other species, like shortspine thornyhead *Sebastolobus alascanus* and sablefish *Anoplopoma fimbria*, that undergo ontogenetic migration from shallow into deep water.

Dover sole *Microstomus pacificus* is a pleuronectid flatfish believed to be long lived (up to 58 years) and found at depths of about 55 m to more than 1,500 m off the west coast of North America (Hunter et al. 1990). Biological characteristics of Dover sole (age, size, sexual maturity, water content, caloric density, and biomass) and key characteristics of their habitat, such as temperature and oxygen concentration, vary with depth (Hunter et al. 1990). Depth-specific properties of Dover sole are becoming increasingly important to fishery managers as bottom-trawl fisheries on the continental shelf expand into deeper water over the continental slope.

Dover sole, like other commercially important species harvested on the continental slope off North America (e.g., shortspine thornyhead *Sebastolobus alascanus* and sablefish *Anoplopoma fimbria*), settle onto the continental shelf as juveniles and then move into deeper water as they age and grow. Some Dover soles eventually move down into the "oxygen minimum zone" where concentrations of dissolved oxygen may be less than 0.5 mL/L (Hunter et al. 1990; also see below). Superimposed on the ontogenetic movement of Dover sole into deep water is a seasonal inshore and offshore movement pattern that has been described in general terms but not precisely quantified (Alverson 1960; Quirollo and Kalvass 1987).

Dover soles undergo profound physiological changes as they grow and move into deeper water. Water content of Dover soles off central California, for example, increases with size, age, and depth from about 82 to 90%, causing a decline in energy content per gram wet weight. Large Dover soles taken from deep water often have "jellied" flesh with water content so high that marketability is affected (Hendrickson et al. 1986).

Ontogenetic movements of Dover sole (and other species harvested on the continental slope) are important in a practical as well as biological sense. Dover sole supports a valuable fishery on the western coast of the United States with annual landings and ex-vessel value during 1982 to 1989 averaging about 19,000 tonnes and US$3 million (1989 dollars). In recent years, the fishery for Dover sole has extended into deeper waters of the continental slope, resulting in increased harvest of older and larger fish (Turnock and Methot 1991). Changes in the depth of commercial fishing have complicated management of Dover sole stocks because effects on age- and size-composition data due to fishing mortality are confounded with effects due to changes in recruitment, mortality, and depth of fishing. It would be difficult, for example, to determine if a reduction in the number of small Dover soles in catches was due to reduced recruitment or a shift in the fishery to deeper water. Stock assessment models that partition fishing mortality rates into year- and age-specific components (e.g., Doubleday 1976; Deriso et al. 1985; Gavaris 1988; Turnock and Methot 1991) assume that age-specific vulnerability to the fishery is constant over time; this assumption may not be valid if the oldest fish are found in the deepest water and the depth at which most fishing takes place has changed. As shown below, an understanding of ontogenetic movements could be used by fishery managers to better manage species like Dover sole.

In this paper we describe biological relationships between size and depth for Dover sole and discuss how this information might be used by fishery managers. First, we develop a simple method for estimating joint, conditional, and marginal probability distributions that are used to describe relationships between depth and length of Dover sole at sites off Oregon and central California. We then show how preferred depth range changes with size at both localities. Next, we use probability distributions for Dover sole and information from commercial fishery logbooks in a simple model to demonstrate effects on fishery length-composition data due to changes in the depth of fishing. We use probability distributions throughout the paper because they naturally describe relationships between size of Dover sole and depth, are mathematically convenient, can be presented graphically, and could be incorporated directly into stock assessment models used by fishery managers. The paper concludes with a discussion of how our results apply to interpretation of other types of fishery data, such as catch rates and age-composition information, and to other species that undergo ontogenetic migrations into deeper water.

## Model

Our approach was based on an estimate of the probability distribution

$$p_t(l, d) = p_t(l \mid d) p_t(d), \tag{1}$$

where $p_t(.)$ is the probability at time $t$ of the event in parentheses, $d$ is the event that a Dover sole is at depth $d$, and $l$ is the event that a Dover sole is length $l$. In the language of probability, $p_t(l, d)$ is the joint probability distribution for depth and length of Dover sole at time $t$ or, in plain terms, the odds that a fish randomly chosen at time $t$ would be length $l$ and at depth $d$. The probability distribution $p_t(d)$ gives the odds that a randomly chosen Dover sole would be at depth $d$ and is called the marginal distribution for depth because it can be obtained by summing elements in the joint distribution across length categories. The probability distribution $p_t(l \mid d)$ gives the odds that a randomly chosen Dover sole would be length $l$ given that it was already at depth $d$ and is called the conditional distribution for length given depth. Expression of a joint probability as the product of marginal and conditional probabilities is a well-known result described in many textbooks (Stuart and Ord 1987: Section 7.7). Length-composition data (aggregated by depth strata) from trawl surveys were used as estimates of the conditional probability distribution for length given depth, $p_t(l \mid d)$, in equation (1).

Catch rates from trawl surveys and bathymetric data were used to estimate the marginal probability distribution for depth of Dover sole, $p_t(d)$, in equation (1):

$$p_t(d) = \frac{f_{t,d} A_d}{\sum_{d=1}^{d_{\max}} f_{t,d} A_d}, \tag{2}$$

where $f_{t,d}$ is the catch rate (number of fish/km$^2$) at depth $d$ and time $t$ (during the survey), and $A_d$ is the surface area of the ocean (km$^2$) above depth stratum $d$. Catch rates were computed as the sum of the number of Dover sole caught during positive tows in a stratum divided by total area swept (distance trawled multiplied by width of the trawl).

The joint probability distribution for depth and length, $p_t(l, d)$, was useful because it concisely summarized bathymetric and survey data and could be used, as shown below, to make informative graphs. Hunter et al. (1990) plotted mean lengths against depth for male and female Dover soles taken off central California using the same data that were used in this study, but their approach obscured some details about relationships between depth and length.

Most conditional and marginal distributions associated with the joint distribution, $p_t(l, d)$, are familiar to fishery scientists and managers. The marginal distribution for depth, $p_t(d)$, is, for example, also known as relative abundance at depth *d*, and the conditional distribution for length given depth, $p_t(l \mid d)$, is also known as the population length composition for depth interval *d*. The marginal distribution for length, $p_t(l)$, which is obtained from equation (1) by summing over depth intervals (see below), is often calculated and used as an estimate of the population length composition.

The major benefit in estimating the joint probability for depth and length of Dover sole, $p_t(l, d)$, was that conditional probability distributions for depth given length could be calculated from the joint distribution using Bayes' theorem (Stuart and Ord 1987):

$$p(d \mid l) = \frac{p_t(l, d)}{p_t(l)}, \tag{3}$$

where $p(d \mid l)$ is the conditional probability at time *t* for depth given length or, in plain terms, the odds that a Dover sole of length *l* would be at depth *d*. These conditional distributions were of particular interest because they reflect preferred depth distributions for Dover sole of different sizes and can be used to show how depth distribution changes as fish grow.

We hypothesize that conditional distributions for depth given length, $p(d \mid l)$, for Dover sole in a particular area are relatively constant over time. This hypotheses is important because, if true, our estimates of conditional distributions for depth given length measure preferred depth distributions as an intrinsic characteristic of Dover sole in a particular area. Estimates of preferred depth distribution might, for example, be incorporated into stock assessment models to enhance management. As shown below, distributions for depth given length differ among localities with different bathymetric characteristics, so habitat probably affects the ontogenetic movement of Dover sole into deep water. Density-dependent effects due to recruitment, mortality, and growth may also affect preferred depth distributions, but it is possible that density-dependent effects are modest relative to ontogenetic and habitat effects. We omit the subscript for time in the expression $p(d \mid l)$ to emphasize this important hypothesis—the temporal consistency of depth given length—although we were unable to prove or disprove it.

The probability distribution for length, $p_t(l)$, in the denominator of equation (3) is a marginal distribution described above. It can be obtained by summing the joint distribution for depth and length, $p_t(l, d)$, over depths:

$$p(l) = \sum_{d=1}^{d_{\max}} p_t(l, d). \tag{4}$$

An important assumption in the mathematical development of our methods was that all Dover soles, regardless of size, were equally catchable by trawls used for research surveys. Cod ends in trawls used for research surveys were lined with small mesh to retain as many small fish as possible, and we omitted data for small and large length-groups with fewer than 20 observations (see below). No net is equally effective for fish of widely different sizes, however, so the assumption of constant catchability was not completely met. Thus, probability distributions estimated from trawl survey data differ from the true population probability distributions for Dover sole, particularly for small fish. Fortunately, modest failures of the assumption of constant catchability would not affect our general conclusions, which were qualitative in nature and based on obvious patterns in the data.

We estimated joint, conditional, and marginal probability distributions separately for males and females as well as for males and females together. Separate analyses were used to characterize differences between the sexes, and the combined analyses were used to examine distributions for all of the Dover soles in one area.

## Data

We used data from bottom-trawl research surveys conducted by the National Marine Fisheries Service (NMFS) in two areas. Data were collected during two bottom-trawl surveys conducted by the RV *David Starr Jordan* off central California (34°30′–37°30′N) at depths of 69–1,295 m during January–February 1987 and February–April 1988

TABLE 1.—Minimum and maximum total lengths ($l$) for Dover sole in joint probability distributions before and after exclusion of length-groups with fewer than 20 observations. Also given are the percentages of the original joint probability distribution (percent probability) eliminated by excluding length-groups with fewer than 20 observations.

| Length criteria and analytical loss | Central California | Oregon |
|---|---|---|
| Before sample exclusion | | |
| Minimum length ($l$, cm) | 8 | 19 |
| Maximum length ($l$, cm) | 55 | 61 |
| After sample exclusion | | |
| Minimum length ($l_{LO}$, cm) | 12 | 25 |
| Maximum length ($l_{HI}$, cm) | 50 | 52 |
| Percent probability | 1.6% | 1.4% |

(Jacobson and Hunter 1992: Appendix Table 1). Data from the two surveys were combined to increase sample size. Although there were some differences between data from the two surveys, general patterns in the distribution of Dover sole by length, depth, and sex were consistent. Surveys were conducted during the spring of two successive years so seasonal and interannual effects on the data should be minimal. A standard NMFS 400-mesh Eastern otter trawl was used for all tows off central california that were included in our analysis (data for unsuccessful tows or tows made with other gear were not used). Detailed descriptions of cruise activities, nets, and sampling procedures are available from Butler et al. (1989), Hunter et al. (1992), and NMFS (Southwest Fisheries Science Center, Post Office Box 271, La Jolla, California 92038). Length-composition, sex, and catch rate (number of Dover soles per kilometer trawled) data were aggregated into seven 200-m depth strata (70–200 m, 200–400 m, 400–600 m, 600–800 m, 800–1,000 m, 1,000–1,200 m, and 1,200–1,400 m). Cruises off central California were conducted during the spawning season for Dover sole, which extends from January to May (Hunter et al. 1992).

We also used data collected during two bottom-trawl surveys conducted by the RV *Miller Freemen* during November–December 1988 and by the FV *Golden Fleece* during September–October 1989 (Jacobson and Hunter 1992: Appendix Table 2). Data from two cruises were combined in order to increase sample size. Although there were some differences between data from the two surveys, general patterns in the distribution of Dover sole by length, depth, and sex were consistent. The surveys were conducted off Oregon (44°–45°30′N) at depths of 194–1,231 m. Length-composition, sex, and catch rate data were aggregated into seven 200-m depth strata (100–200 m, 200–400 m, 400–600 m, 600–800 m, 800–1,000 m, 1,000–1,200 m, and 1,200–1,400 m). Data for two tows at depths of 194–200 m were extrapolated to the entire 100–200-m stratum so that results for Oregon would be as comparable as possible to results for central California. A standard NMFS poly Nor'eastern otter trawl was used for all tows in both Oregon surveys. Detailed descriptions of cruise activities, nets, and sampling procedures are available from Hunter et al. (1992) and NMFS (Alaska Fisheries Science Center, 7600 Sand Point Way NE, BIN C15700, Seattle, Washington 98115). Cruises off Oregon were conducted just prior to the January–May spawning season for Dover sole.

The smallest and largest length-classes at each area were undersampled (contained fewer than 20 Dover soles; Jacobson and Hunter 1992: Appendix Tables 1, 2). Undersampling of small fish may have been due to reduced catchability of small fish or lack of trawling in very shallow water (less than 69 m off central California and less than 194 m off Oregon), where small fish are most abundant. Undersampling of large fish was probably due to their low abundance and too few tows in deep water. We avoided irregularities in probability distributions due to small sample sizes by excluding length-classes with fewer than 20 fish from the joint probability distributions of equation (1) and normalizing:

$$p_t'(l, d) = \frac{p_t(l, d)}{\sum_{d=1}^{d_{\max}} \sum_{l=l_{LO}}^{l_{HI}} p_t(l, d)}; \qquad (5)$$

where $p_t'(l, d)$ was the normalized joint probability, $l_{LO}$ and $l_{HI}$ were the first and last length-groups with at least 20 observations included in the normalized distribution, and length-groups ($l$) were restricted to the interval ($l_{LO}$, $l_{HI}$). Little information was lost by normalizing because less than 2% of the original joint probability distributions were excluded (Table 1).

Bathymetric data for Dover sole habitat at the two study sites were obtained by digitizing contours on standard bathymetric charts. For both study sites, we calculated the area (km$^2$) within each depth interval (boundaries of study sites and depth intervals defined above).

There were pronounced differences in bathymetry between the two study areas (Figure 1; Jacobson and Hunter 1992: Appendix Tables 1, 2). Dover sole habitat (approximately 50–1,500 m in

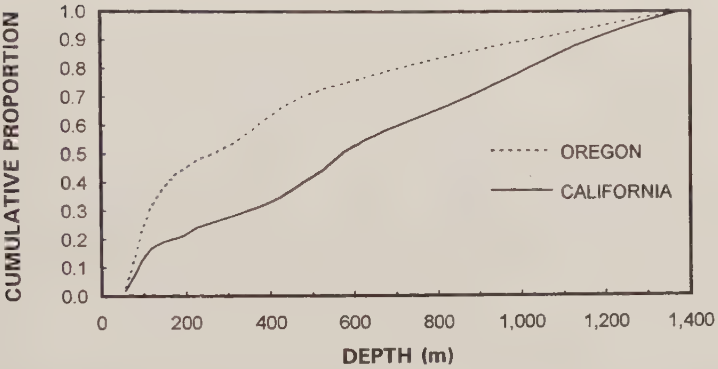

FIGURE 1.—Cumulative probability plots for area and depth of Dover sole habitat in the central California and Oregon study areas. The plots show the cumulative proportion of the total habitat area at or shallower than a given depth. For example, about 64% and 83% of total study areas in central California and Oregon were shallower than 800 m.

depth) was narrow off central California and wider off Oregon. For example, 70% of total area in the central California site is deeper than 400 m compared with only 40% of the total area in the Oregon site. These differences allowed us to make a preliminary assessment of the effects of habitat bathymetry on depth and length of Dover sole. The assessment was preliminary because the two areas were sampled at different times of the year, and effects of seasons and bathymetry may be confounded in our data.

## Results and Discussion

Joint probability distributions for both areas (Hunter et al. 1990; Jacobson and Hunter 1992: Appendix Tables 3, 4) show that female Dover soles grow to larger size than males. In both areas female Dover soles longer than 45 cm in total length (TL) were frequently seen but males longer than 45 cm TL were seldom encountered (Figures 2, 3).

### *Relationships between Sex, Depth, and Area*

Percent female Dover soles increased with depth at both sites such that individuals at 1,200–1,400 m were 96% female (Figure 4; Table 2). We used logistic regression implemented as a generalized linear model, or GLIM (McCullagh and Nelder 1983; Chambers and Hastie 1992), to test the statistical significance of this pattern at both sites as well as to test for differences between cruises at the same site and statistical interactions. An advantage of the GLIM approach is that overdispersion in the data can be estimated with quasi-likelihood techniques (McCullagh and Nelder 1983). Quasi-likelihood estimates for logistic regression parameters were the same as normal maximum-likelihood estimates except that an estimate of the ratio of observed and expected sampling variances ($\phi$, the dispersion parameter) was obtained. In our analysis, for example, the sample variance for the fraction female in each tow was assumed to be $\phi f(1 - f)/N$ (where $f$ is fraction female and $N$ is the number of fish sampled) instead of $f(1 - f)/N$, which would be expected for a binomial random variable like the fraction of female Dover soles. Logistic regression models for each site treated depth as a covariate (continuous variable) and cruises as factors (categorical variables); $F$-tests (McCullagh and Nelder 1983) were used to judge the statistical importance of interactions, factors, and covariates because the data were found to be overdispersed ($\phi > 1$).

Interaction terms and cruises were insignificant for Dover sole at both sites (two-tailed $P < 0.14$), so final models for each site included depth effects only (Figure 4). Depth was statistically significant ($P < 0.001$) in the models for both sites, indicating that the proportion of female Dover soles at both sites increased with depth.

Variation in sex ratios for Dover soles taken in different tows at the same depth and site was larger than expected. The ratio of actual to expected sampling variance (as measured by the dispersion parameter $\phi$ in GLIM) was 5.5 for the Oregon site and 7.0 at the central California site. This indicates that Dover soles at a particular depth in a particular area were not randomly distributed by sex. Instead, groups of Dover soles that were predominantly male or female tended to occur in patches

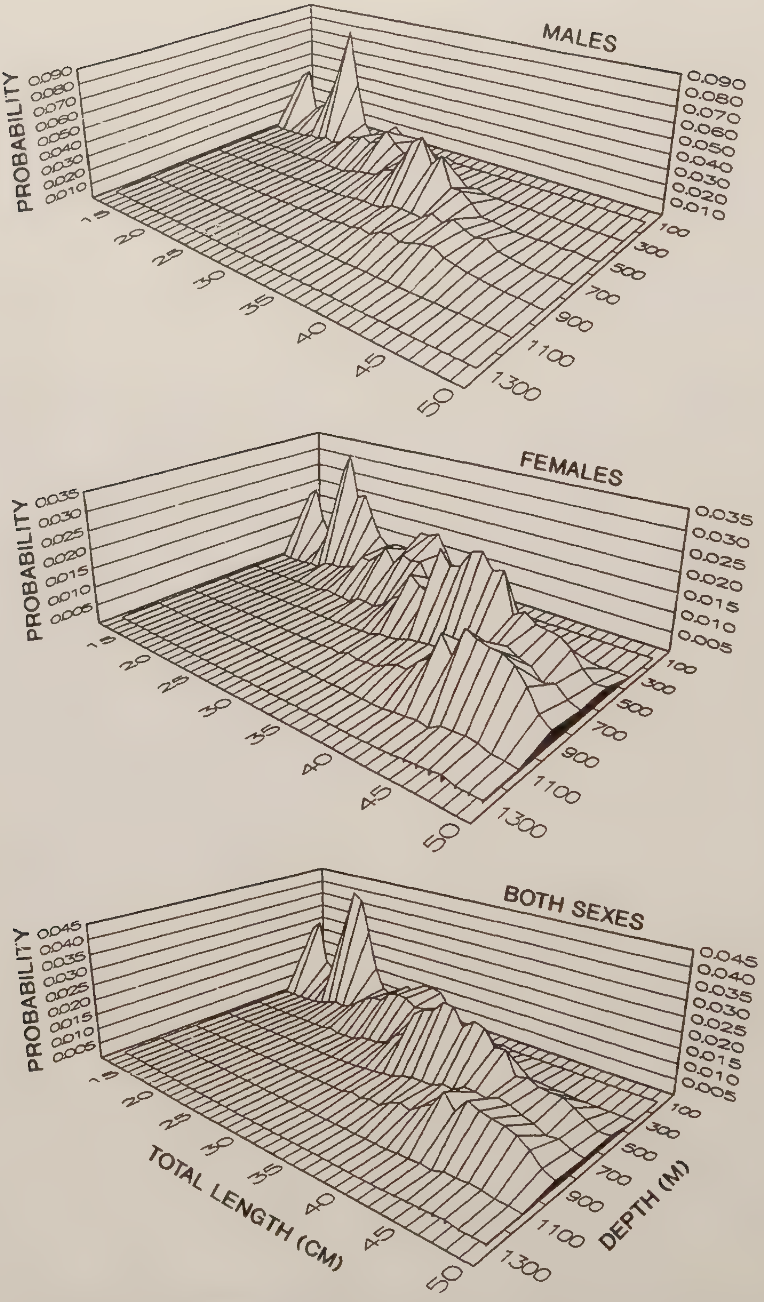

FIGURE 2.—Joint probability distributions for depth and length of Dover soles ($p_t'[l, d]$, exclusive of length-classes with fewer than 20 observations) in the central California study area based on bathymetric data and research trawl surveys conducted during January–February 1987 and February–April 1988. Distributions for males, females, and combined sexes are shown.

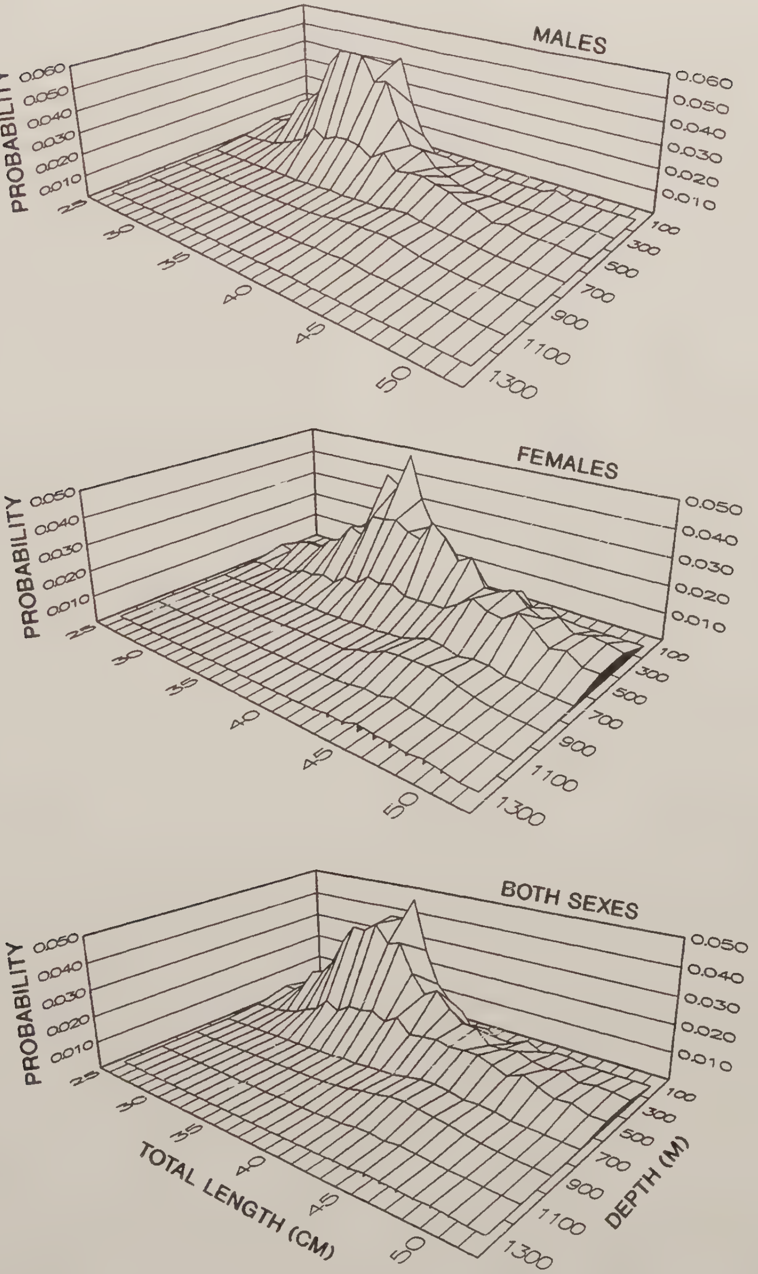

FIGURE 3.—Joint probability distributions for depth and length of Dover soles ($p_t'[l, d]$, exclusive of length-classes with fewer than 20 observations) in the Oregon study area based on bathymetric data and research trawl surveys conducted during November–December 1988 and September–October 1989. Distributions for males, females, and combined sexes are shown.

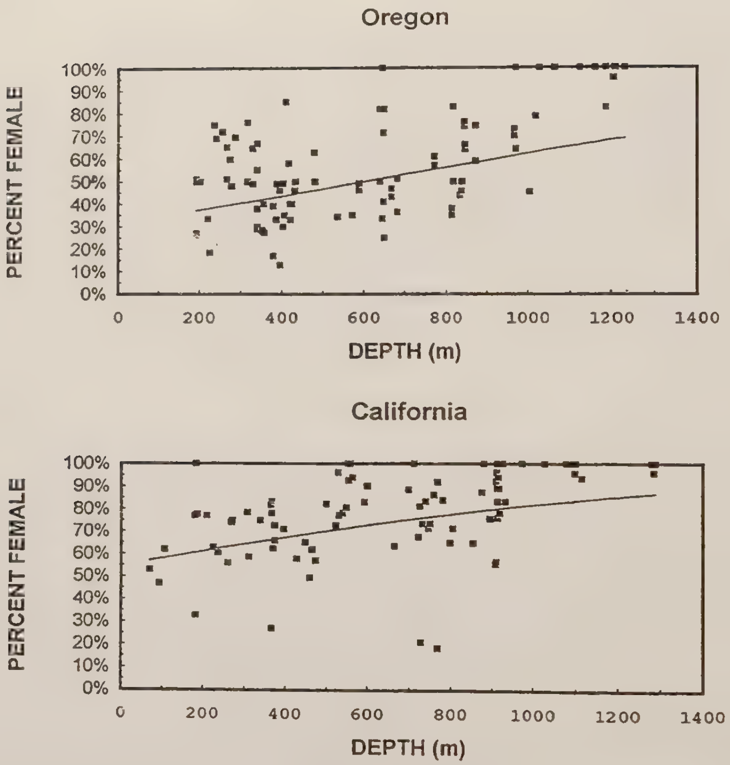

FIGURE 4.—Sex ratios for Dover soles taken during Oregon and central California surveys. Shown are data for individual tows and lines fitted by logistic regression analyses.

sampled by different tows. Dover soles were taken off central California during their spawning season and off Oregon just prior to their spawning season. It seems likely that excess variability in sex ratios was due to spawning behavior, particularly because there was more excess variability in sex ratios of Dover soles taken off central California during the peak spawning season. Unbalanced sex ratios are associated with spawning behavior of other fish species (Hunter and Goldberg 1980). Among northern anchovies *Engraulis mordax*, for example, most spawning females are found in male-dominated schools.

A larger proportion of female Dover soles live in deep water. The proportion of females living at depths greater than 600 m, for example, was 11% at the Oregon site and 27% at the central California site, whereas the proportion of males at depths greater than 600 m was 7% at the Oregon site and 19% at the central California site (Table 3).

There were marked differences in overall sex ratios between sites. Females were 67% of the total population at the central California site but only 43% of the total population at the Oregon site. The differences in sex ratio did not appear to be a sampling artifact or other error because the pattern was consistent for both cruises at each site and across depth intervals (Table 3).

### *Ontogenetic Movements*

General patterns in the ontogenetic movement of immature Dover soles from shallow into deep water were similar for males and females in both areas (Figures 5, 6). Conditional distributions for depth given length $p_l(d \mid l)$, indicated that young Dover soles off central California remain in water less than 200 m deep until they are about 23 cm TL; then an abrupt shift into deeper water (300–400 m) occurs (Figure 5). No information about Dover soles less than 25 cm TL was available for the Oregon site. After the first transition at 23 cm TL, depth preferences of Dover soles off central California did not change until a second, more

TABLE 2.—Percentages of female Dover soles by depth interval and cruise. Values for depth intervals are means for individual tows in each interval weighted by sample size (number of fish sexed). Totals are means for depth strata weighted by catch rate and depth stratum size. Sample sizes are given in parentheses.

| | Percent female Dover sole ($N$) | | |
|---|---|---|---|
| Depth (m) | First cruise | Second cruise | Both cruises |
| **Oregon (Nov-Dec 1988; Sep-Oct 1989)** | | | |
| 100–200 | 50% (6) | 39% (200) | 39% (206) |
| 200–400 | 47% (915) | 39% (1,162) | 42% (2,077) |
| 400–600 | 43% (648) | 45% (531) | 44% (1,179) |
| 600–800 | 49% (261) | 51% (382) | 50% (643) |
| 800–1,000 | 60% (641) | 55% (653) | 58% (1,294) |
| 1,000–1,200 | 79% (112) | 49% (104) | 65% (216) |
| 1,200–1,400 | 96% (53) | 100% (2) | 96% (55) |
| Total | 48% (2,636) | 41% (3,304) | 43% (5,670) |
| **Central California (Jan-Feb 1987; Feb-Apr 1988)** | | | |
| 70–200 | 72% (47) | 55% (64) | 62% (111) |
| 200–400 | 64% (96) | 58% (291) | 60% (387) |
| 400–600 | 84% (77) | 67% (270) | 71% (347) |
| 600–800 | 70% (143) | 64% (174) | 67% (317) |
| 800–1,000 | 73% (203) | 79% (71) | 74% (274) |
| 1,000–1,200 | 93% (42) | 100% (6) | 94% (48) |
| 1,200–1,400 | 96% (23) | (0) | 96% (23) |
| Total | 74% (631) | 61% (876) | 67% (1,507) |

TABLE 3.—Probabilities and cumulative probabilities (in parentheses) of Dover sole occurrence by sex and depth interval in the central California and Oregon areas. The probabilities in the table are the same as $p_l(d)$ in equation (1). For example, 41% of male Dover soles in the Oregon area were between 200 and 400 m and 31% + 41% = 72% were in water less than 400 m deep.

| | Probability of occurrence | | |
|---|---|---|---|
| Depth (m) | Male | Female | Both sexes |
| **Oregon** | | | |
| 100–200 | 0.31 | 0.27 | 0.29 |
| 200–400 | 0.41 (0.72) | 0.42 (0.69) | 0.43 (0.72) |
| 400–600 | 0.21 (0.93) | 0.20 (0.89) | 0.20 (0.92) |
| 600–800 | 0.03 (0.96) | 0.04 (0.93) | 0.03 (0.95) |
| 800–1,000 | 0.03 (0.99) | 0.05 (0.98) | 0.03 (0.98) |
| 1,000–1,200 | 0.01 (1.00) | 0.02 (1.00) | 0.01 (0.99) |
| 1,200–1,400 | 0.00 (1.00) | 0.00 (1.00) | 0.01 (1.00) |
| **Central California** | | | |
| 70–200 | 0.39 | 0.30 | 0.33 |
| 200–400 | 0.17 (0.56) | 0.15 (0.45) | 0.15 (0.48) |
| 400–600 | 0.25 (0.81) | 0.28 (0.73) | 0.28 (0.76) |
| 600–800 | 0.10 (0.91) | 0.10 (0.83) | 0.10 (0.86) |
| 800–1,000 | 0.08 (0.99) | 0.15 (0.98) | 0.13 (0.99) |
| 1,000–1,200 | 0.00 (1.00) | 0.01 (0.99) | 0.01 (1.00) |
| 1,200–1,400 | 0.00 (1.00) | 0.01 (1.00) | 0.00 (1.00) |

gradual, transition into deeper water (800–1,000 m) occurred at about 30–33 cm TL (Figure 5). Off Oregon, the first transition to deeper water occurred at about 37 cm TL (Figure 6). The transitions at 30–37 cm TL may be related to sexual maturity, because the length at which 50% of female Dover soles at both study sites reach sexual maturity is about 33 cm TL (Hunter et al. 1992).

Movements of sexually mature Dover soles into deeper water were similar in both areas although differences existed between the sites in the extent to which fish moved to depths beyond 800 m (Figures 5, 6). In both areas Dover soles gradually moved into deeper water as fish grew beyond the length of initial sexual maturity, and a considerable number of fish were found at depths of 800–1,000 m by the time Dover soles in both areas reached 40 cm TL. Conditional depth distributions, $p(d \mid l)$, for male and female Dover soles larger than 40 cm TL in both areas show a depression at approximately the depth range (600–800 m), where oxygen concentrations are lowest (Figures 5–7). This pattern was especially pronounced off central California, where more Dover soles are found in deep water and the zone of minimum oxygen is narrower (Figure 7), but was evident in the conditional probability distributions for both areas (Figures 5, 6). Lower probabilities indicate that Dover soles migrate through but may not remain for long at depths where oxygen concentrations are lowest.

Most Dover soles larger than 40 cm TL in the central California area were found below the oxygen minimum at depths greater than 800 m, whereas most fish larger than 40 cm TL in the Oregon area were found above the oxygen minimum at depths less than 600 m (Figure 7). This difference may have been due to differences in topography; less shallow-water habitat is available off central California than off Oregon (Figure 1), although other explanations, such as seasonal migration and intraspecific competition (density of Dover soles and food availability), are also plausible.

### *Effect of Fishing Depth on Fishery Data*

We used the joint probability densities, $p(d, l)$, for depth and length of male and female Dover soles in the central California and Oregon areas along with logbook data in a simple model to investigate effects of changes in the depth of fishing on fishery length-composition data. In the model, we assumed that the population length composition was the same as estimated from the trawl surveys; that is, that the population length com-

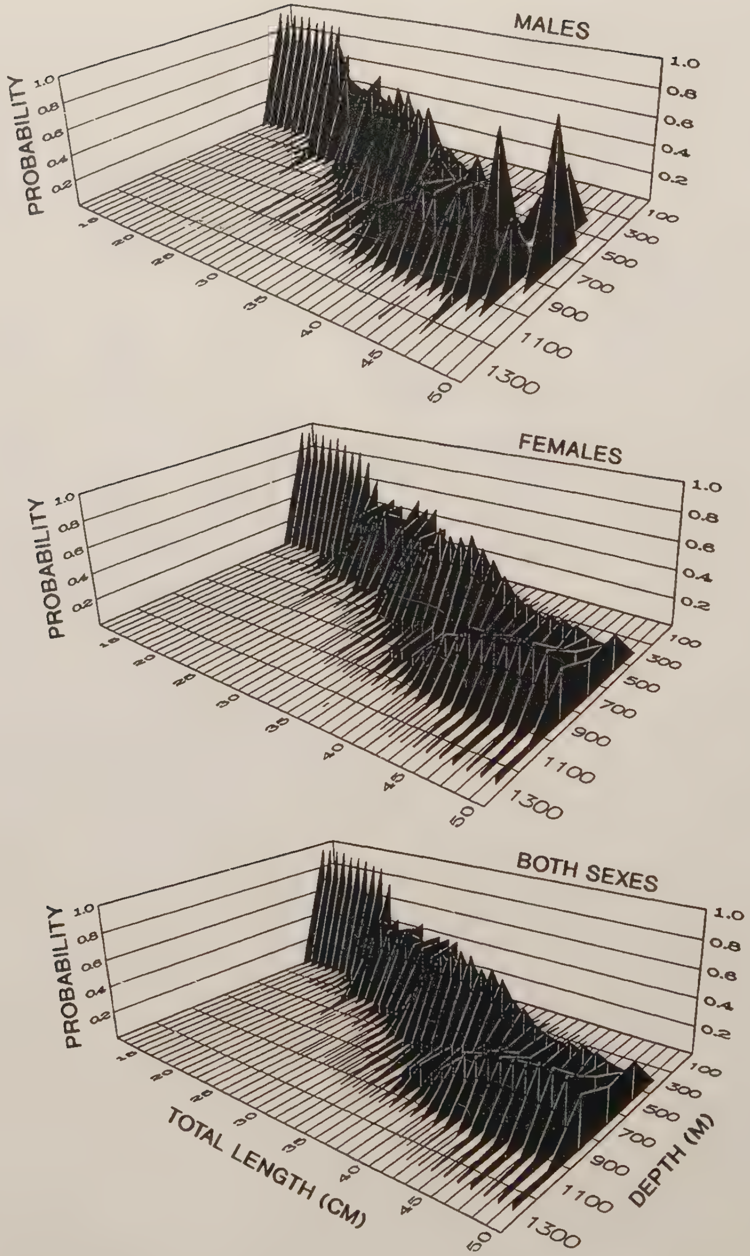

FIGURE 5.—Conditional probability distributions for depth of Dover soles given length ($p[d \mid l]$, exclusive of length-classes with fewer than 20 observations) in the central California study area. Distributions for males, females, and sexes combined are shown. Conditional distributions are given for each 1-cm length-group.

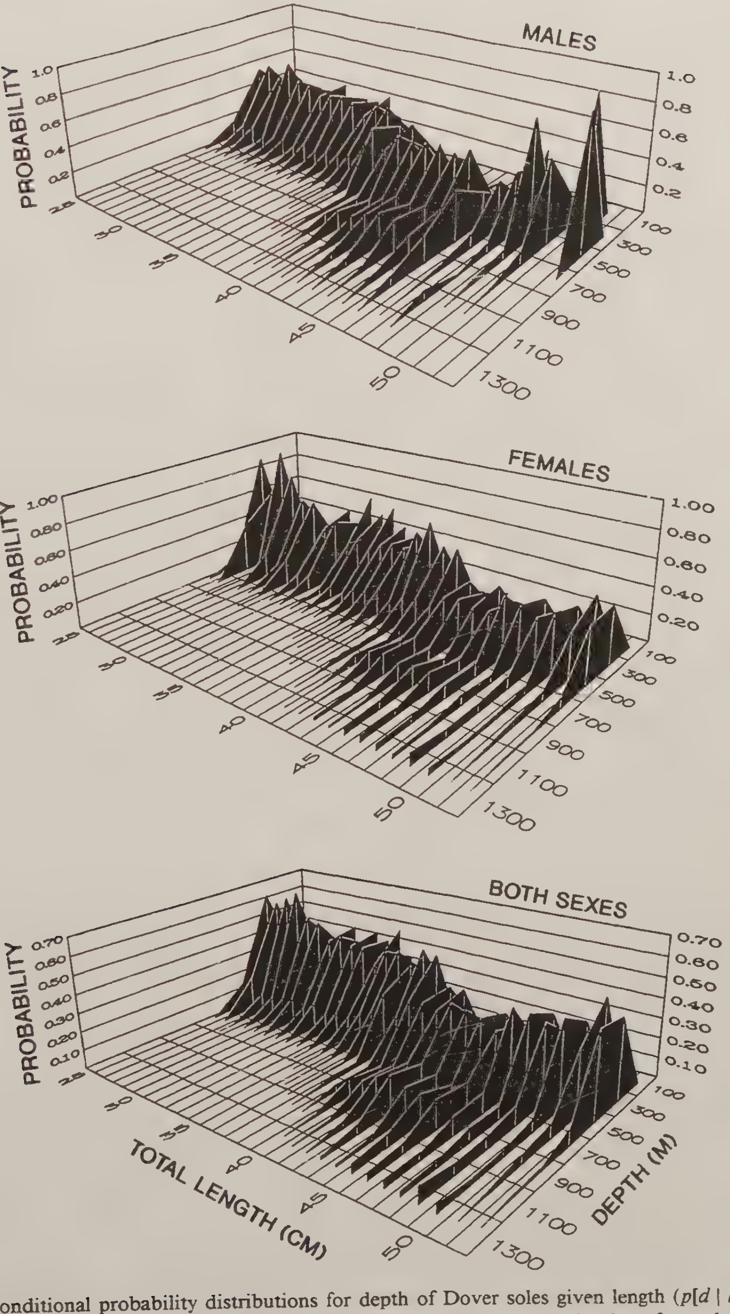

FIGURE 6.—Conditional probability distributions for depth of Dover soles given length ($p[d \mid l]$, exclusive of length-classes with fewer than 20 observations) in the Oregon study area. Distributions for males, females, and sexes combined are shown. Conditional distributions are given for each 1-cm length-group.

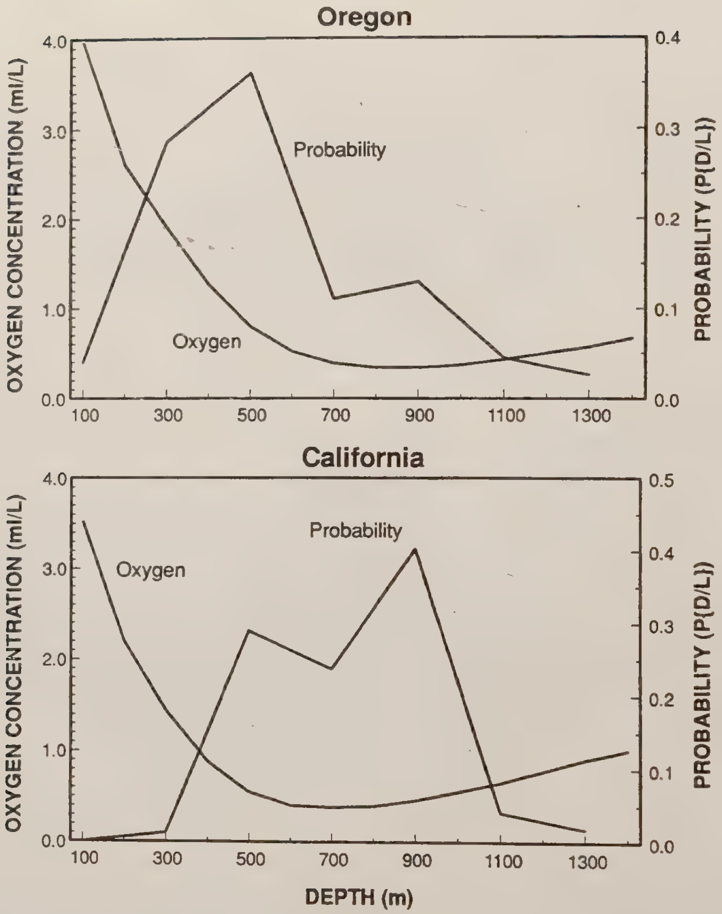

FIGURE 7.—Oxygen concentration as a function of depth in the Oregon and central California study areas and marginal probabilities for depth of Dover soles larger than 40 cm total length ($p[d \mid l > 40 \text{ cm}]$). Oxygen data were obtained from an atlas and are means for observations recorded during January–December 1920–1970 (Churgin and Halminski 1974). Oxygen data for Oregon are from the area 44–46°N and 123–127°W. Oxygen data for central California are from the area 34–36°N and 118–125°W and the area 36–38°N and 121–126°W.

position was $p_t(l)$ from equation (1). We also assumed that the probability of capture (catchability) for a Dover sole lying in the path of a commercial trawl was independent of the size of the fish. The final assumption was that probability of capture in a depth stratum was proportional to the product of fishing effort (adjusted as described below) and abundance of Dover sole in the stratum:

$$\begin{aligned} p_t(c, d, l) &= p_t(d, l)p_t(c \mid d, l) \\ &= p_t(d, l)qE_{d,t}, \end{aligned} \tag{6}$$

where $c$ denotes capture, $E_{d,t}$ is the amount of fishing effort at depth $d$ and time $t$, and $q$ is the catchability coefficient. The assumption of constant catchability for all sizes of Dover soles does not hold for bottom trawls used by the commercial fishery, but this issue was not important in our analysis because the model was meant to show general patterns only.

The assumptions described above led to a convenient formula for calculating the length composition of the catch (conditional probability distribution for length given capture, $p_t[l \mid c]$) in our model:

$$p_t(l \mid c) = \frac{p_t(l, c)}{p_t(c)} = \frac{\sum_{d=1}^{d_{\max}} p_t(c, d, l)}{\sum_{l=1}^{l_{\max}} \sum_{d=1}^{d_{\max}} p_t(c, d, l)}. \quad (7)$$

Nominal fishing effort data (hours fished) from logbooks for bottom-trawl fishing during 1978 and 1987 in the Columbia management area off Oregon (43°–47°30′N) and the Monterey management area off central California (36°–40°30′N) were used. The fishing effort data were for areas that encompassed the area of the Oregon and central California trawl surveys and showed the shift of the bottom-trawl fishery in the two areas from shallow to deeper water (Table 4). Total hours fished in each depth stratum were calculated by summing effort for all trips in which any Dover soles were taken. Total hours in each stratum was then divided by the area (km$^2$) of the stratum in order to express fishing effort in each stratum on a per area basis (h/km). This was necessary because the probability of capturing a Dover sole during 1 h of trawling in a small area is greater than the probability of capture during 1 h of trawling in a large area. The adjusted measure of effort in each stratum was then converted to a percentage of total adjusted effort because only the relative amount of fishing effort in each stratum was important (Table 4).

Results from the model (Figure 8) indicate that fishery length-composition data for species like Dover sole can differ from the underlying population length composition. This result makes sense because a fishery in shallow water will tend to take small fish and a fishery in deep water will tend to take large fish irrespective of the population length composition. Differences between fishery and population length compositions may be modest, as in our model of the Oregon fishery, or substantial, as in our model of the central California fishery. These differences can be expected even, as in our demonstration, when catchability is the same for all size-classes unless the amount of nominal fishing effort in each stratum is inversely proportional to stratum size, so that fish at all depths experience the same fishing mortality.

Relationships between population and fishery length compositions are sensitive to changes in the distribution of fishing effort with depth (Figure 8) and could confound stock assessment and management efforts. This result makes sense because movement of the fishery to deeper water would result in more large fish caught and movement of the fishery into shallow water would result in more small fish caught, irrespective of the population length composition. Our results indicate that increased fishing effort in deeper water by the bottom-trawl fishery off Oregon and, particularly, central California between 1978 and 1987 would have resulted in changes in fishery length-composition data even if the underlying length composition of the population did not change. Length-composition data from the central California fishery for 1978 and 1987 from our model would indicate, if used in a stock-assessment analysis without information about the distribution of fishing effort with depth, reduced recruitment in later years, increased mortality of young fish, or an increase in the survival of larger fish. The consequences of this error in perception might well be erroneous recommendations to managers.

TABLE 4.—Percent nominal fishing effort (h) and adjusted fishing effort (h/km) by depth stratum in the central California and Oregon areas by commercial bottom-trawl fisheries, 1978 and 1987.

| | | Percent fishing effort | | | |
|---|---|---|---|---|---|
| | | 1978 | | 1987 | |
| Depth (m) | Area (km$^2$) | Nominal | Adjusted | Nominal | Adjusted |
| **Oregon** | | | | | |
| 100–200 | 2,491 | 40 | 32 | 21 | 15 |
| 200–400 | 1,820 | 54 | 60 | 56 | 57 |
| 400–600 | 1,639 | 5 | 6 | 20 | 22 |
| 600–800 | 919 | 1 | 1 | 3 | 6 |
| 800–1,400 | 1,988 | 0 | 0 | 0 | 0 |
| **Central California** | | | | | |
| 100–200 | 3,436 | 31 | 27 | 16 | 14 |
| 200–400 | 2,005 | 10 | 15 | 8 | 11 |
| 400–600 | 3,858 | 21 | 16 | 24 | 18 |
| 600–800 | 2,729 | 28 | 31 | 31 | 34 |
| 800–1,000 | 2,621 | 9 | 10 | 19 | 21 |
| 1,000–1,200 | 2,726 | 1 | 1 | 2 | 2 |
| 1,200–1,400 | 1,882 | 0 | 0 | 0 | 0 |

## Conclusion

Our analysis shows that Dover soles were not randomly distributed by length, sex, or depth at two study sites. Dover soles at greatest depths in both areas tended to be female, larger (and presumably older), and more often sexually mature than were Dover soles living at shallower depths. Consistency of these patterns among cruises, sampling dates, and sites indicates that our results were not artifacts of sampling, choice of study sites, or

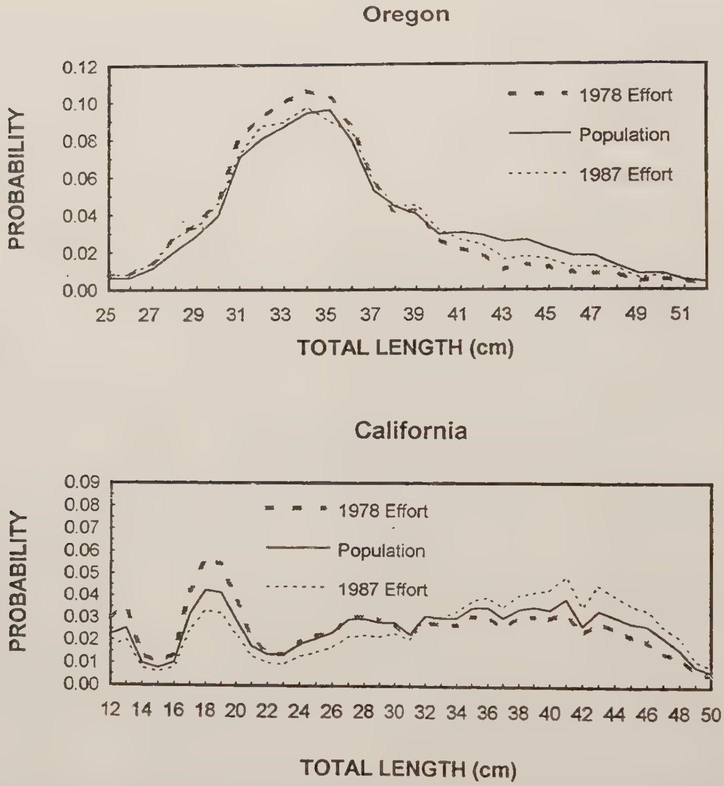

FIGURE 8.—Predicted length compositions from a model of the commercial bottom-trawl fishery in the Oregon and central California study areas during 1978 and 1987.

seasons. Superimposed on the general pattern of increasing size, sexual maturity, and percentage female with depth were local patterns due to topography and oxygen concentration, as well as a great deal of variance in sex ratios of Dover soles taken at different locations in the same depth interval.

Problems in interpreting commercial fishery data caused by relationships between depth and size are not confined to Dover sole. Data for shortspine thornyhead, for example, show relationships between length, depth, sexual maturity, and the oxygen minimum zone similar to those of Dover sole (Figure 9).

Our analysis dealt primarily with effects on fishery length-composition data due to the distribution of fishing effort with depth, but our results can be applied to other types of fishing data as well. For species like Dover sole, fishing effort concentrated in shallow water will tend to oversample young (small) individuals, whereas fishing effort concentrated in deep water will tend to oversample old (large) individuals. A change in the distribution of fishing effort from shallow to deep water will result in age-composition data that indicate reduced recruitment, increased mortality of young (small) fish, or increased survival of old (large) fish even when no change in the underlying population age composition has occurred. Analogously, catch rates from fishing in shallow water will tend to measure the abundance of small young fish, catch rates from fishing in deep water will tend to measure the abundance of large old fish, and a temporal shift in the depth of fishing will complicate interpretation of catch rate data.

It appears difficult to interpret fishery data for species like Dover sole, shortspine thornyheads, and sablefish unless information about the distribution of fishing effort and suitable depth-stratified (and perhaps sex-stratified) models are used. The conditional distributions for depth given length, $p(d \mid l)$, that we obtained for Dover sole

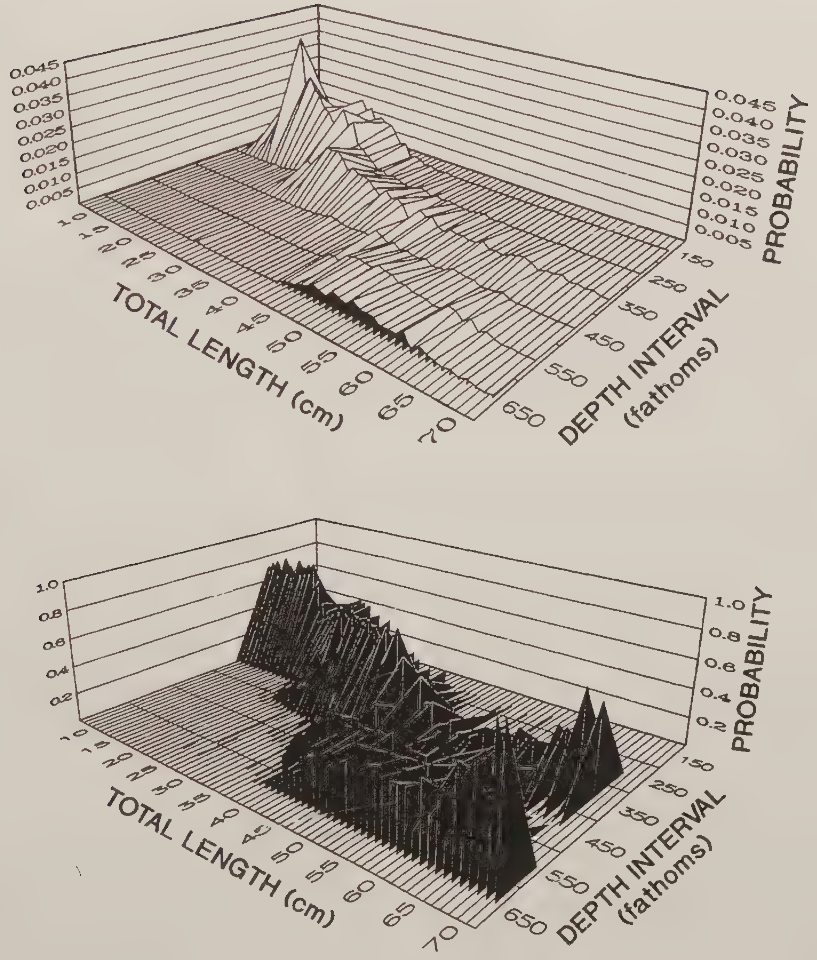

FIGURE 9.—Probability distributions for shortspine thornyhead (both sexes) off the coast of central California during February–April 1988. The top panel shows the joint distribution for depth and length ($p_t'[l, d]$, exclusive of length-classes with fewer than 20 observations). The bottom panel shows conditional distributions for depth given length ($p[d \mid l]$, for length-classes with 20 or more observations).

in the central California and Oregon areas may be useful in the development of suitable models, but information about temporal variation in conditional distributions for depth given length, bathymetry of fishing grounds, depth of fishing, and data from research trawl surveys will also be required.

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# Opportunity Costs and the Decision to Fish for Northern Anchovy

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*Abstract.*—Since 1982, declines in the U.S. reduction fishery for northern anchovy *Engraulis mordax* were due to ex-vessel prices too low to meet opportunity costs of traditional crew members in the southern California wetfish fleet, rather than to inability to meet variable (short-run) costs for items such as fuel. The decline of the fishery appeared to be driven largely by opportunity costs, which, in turn, depended on the ethnic background of crew members. Our analysis indicated that opportunity costs and sociological factors, which are often ignored by fishery managers who traditionally focus on biological analyses, can affect a fishery and its performance. Estimates of opportunity and variable costs from our study should be useful in the development of management plans for the wetfish fishery.

The central population of northern anchovy *Engraulis mordax* ranges from about San Francisco, California, south to Punta Baja, Baja California, Mexico. Northern anchovy have been harvested by U.S. and Mexican fleets for reduction to fish meal and oil primarily, although modest amounts have also been taken for live bait, dead bait, and human consumption. Annual U.S. reduction landings averaged 62,000 tonnes during 1966–1982, but annual landings dropped abruptly in 1983 and averaged only 920 tonnes during 1983–1989 (Figure 1).

Our data and industry sources indicate that the U.S. northern anchovy reduction fishery declined after 1982 because of low ex-vessel prices (prices paid to fishermen by reduction processors), not because of biological or regulatory factors. Ex-vessel prices for northern anchovy landed for reduction in the USA (Table 1) were \$53–103$\cdot$tonne$^{-1}$ during 1974–1982 but only \$29–48$\cdot$tonne$^{-1}$ during 1983–1989. (All monetary values in this article are given in 1989 U.S. dollars). In contrast, northern anchovy biomass levels during 1983–1988 were not low (Methot 1989; Jacobson and Lo 1990) and U.S. reduction landings were less than annual harvest quotas (Thomson et al. 1990).

The purpose of our analysis was to determine the effect of ex-vessel prices on participation in the northern anchovy reduction fishery. We begin by describing the fishing fleet and our data sources. Next, we define variable and fixed costs and explain why our analysis focused on variable costs and short-run business decisions in the fishery. Then, we define opportunity costs, describe two groups of crew members in the wetfish fishery, and estimate opportunity costs for one group. A simple bioeconomic model for earnings by crew members is developed and used to estimate opportunity costs for the second group of crew members.

## Definitions and Background

### *The Fishery*

In terms of total landings, the most important segment of the U.S. reduction fishery for northern anchovy has been the southern California "wetfish fleet" that is based in Los Angeles Harbor and has small segments in the Ventura and Monterey Bay areas (Huppert 1981). In addition to northern anchovy, the fleet harvests chub mackerel *Scomber japonicus*, jack mackerel *Trachurus symmetricus*, Pacific bonito *Sarda chiliensis*, California market squid *Loligo opalescens*, Pacific sardine *Sardinops sagax*, bluefin tuna *Thunnus thynnus*, and other tunas *Thunnus* spp., depending on availability. Fishing for northern anchovy is regulated by the Pacific Fishery Management Council (1983, 1990), whereas fishing for chub mackerel and Pacific sardine is regulated by the state of California (California Department of Fish and Game 1990).

During 1989, the fleet consisted of 38 active purse-seiners averaging 20 m in length (Thomson et al. 1990). Approximately one-third of the fleet was boats with steel hulls built during the last 20 years. The others were boats with wooden hulls built during 1930–1949, the heyday of the Pacific sardine fishery in California (Murphy 1966). The crew on a boat in the wetfish fleet consists of a skipper, who usually owns the boat, an engineer, and other crew members.

During 1983–1989, while ex-vessel prices paid

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[1] Authorship equal and alphabetical.

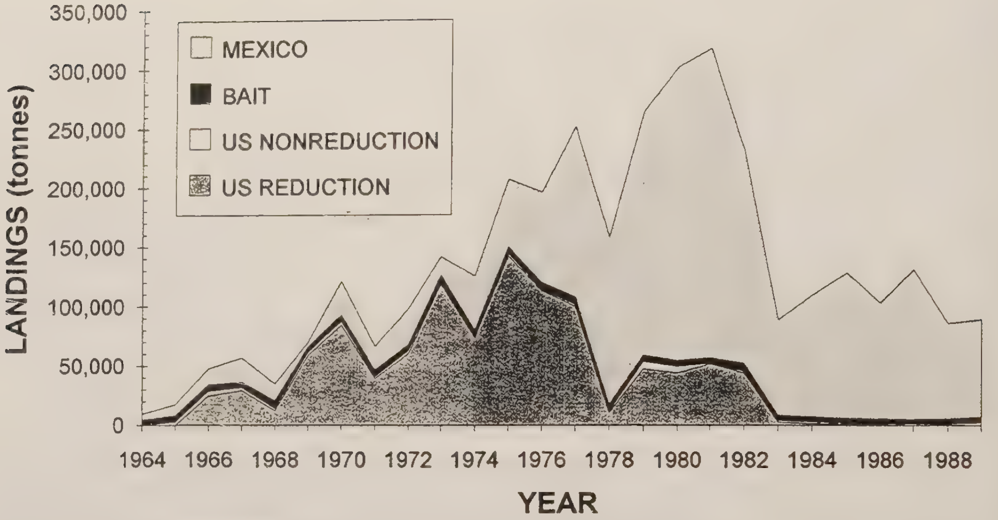

FIGURE 1.—Northern anchovy landings during 1964–1989 by the Mexican reduction fishery, U.S. reduction fishery, U.S. nonreduction commercial fishery, and U.S. live-bait fishery. The U.S. reduction fishery began in 1965.

by reduction processors for northern anchovy were low ($29–48·tonne$^{-1}$; Table 1), ex-vessel prices (per tonne) were $150–200 for mackerels and Pacific sardine, $175–275 for California market squid, $200–450 for Pacific bonito, and $1,000–5,000 for tunas. Because fishing for other species is more lucrative, the wetfish fleet tends to take northern anchovy for reduction as a sideline when other species are not available (Thomson et al. 1990).

TABLE 1.—Landings and ex-vessel prices for northern anchovy in the U.S. reduction fishery, 1974–1989. $ = 1989 U.S. dollars.

| Year | Landing (tonnes) | Price ($·tonne$^{-1}$) |
|---|---|---|
| 1974 | 73,400 | 103 |
| 1975 | 141,586 | 71 |
| 1976 | 112,270 | 79 |
| 1977 | 99,674 | 96 |
| 1978 | 10,339 | 91 |
| 1979 | 47,408 | 80 |
| 1980 | 43,699 | 82 |
| 1981 | 51,290 | 82 |
| 1982 | 43,742 | 53 |
| 1983 | 2,854 | 48 |
| 1984 | 1,722 | 39 |
| 1985 | 825 | 34 |
| 1986 | 546 | 30 |
| 1987 | 149 | 29 |
| 1988 | 234 | 33 |
| 1989 | 109 | 36 |

Mackerels, California market squid, tunas, and Pacific bonito are the mainstay of the fleet during most years. Fishing for Pacific sardine has been allowed since 1986, but until 1990, annual quotas for directed fishing were limited to 2,000 tonnes so that Pacific sardine contributed little to overall landings and revenues (the products of ex-vessel prices and landings) for the wetfish fleet. Mackerels are usually available to the fleet year-round. Pacific bonito, California market squid, and tunas are available to the fishery on a seasonal basis.

### *Data Sources*

Our analysis used financial, socioeconomic, and fishery logbook data for a segment of the wetfish fleet based at the port of San Pedro in the Los Angeles Harbor. Data sources were interviews with boat owners, business records for 1990 provided by the Fishermen's Cooperative Association and by the Fisherman and Allied Workers Union in San Pedro, and logbook data provided by the California Department of Fish and Game. The Fishermen's Cooperative Association and the Fisherman and Allied Workers Union included a substantial fraction (about 25%) of boat owners and fishermen in the wetfish fleet.

Logbook data used in this analysis were for seven of the most modern vessels in the San Pedro wetfish fleet during 1966–1979, which was a period when the U.S. fleet made substantial northern anchovy reduction harvests (Figure 1). More recent logbook data for the wetfish fleet were not available. Information about catch rates and duration of fishing trips for northern anchovy from logbook data for 1966–1979 was probably still valid, because most of the vessels for which logbook data were available were still in operation and boats and equipment used by the fleet had changed little since 1979. We used sensitivity analysis to determine if our results would have been substantially affected by modest changes in the efficiency (catch rates) of boats after 1979.

### *Variable Costs and the Short-Run Decision to Fish*

In economics, business expenses that do not change during a period of interest are deemed "fixed," whereas costs that can change are called "variable." Fuel is the major variable cost in the wetfish fishery. In addition, a certain period is considered "the short run" if some costs are fixed and "the long run" if all costs are variable (Henderson and Quandt 1971). In the long run, according to economic theory, all costs are variable because, for example, boat owners can sell their boats, quit fishing, and avoid mortgage expenses altogether. Theory indicates that, in the short run, boat owners' decisions about how, when, and where to fish will tend to depend on variable costs, such as fuel expenses, but not fixed costs, such as mortgage expenses. The significance of these concepts in our analysis is that boat owners and crew members in the wetfish fleet will tend to fish for northern anchovy as a sideline in the short run only if variable costs and their opportunity costs (described below) can be met. As long as fishing for northern anchovy is a sideline activity, boat owners will meet their fixed costs primarily by fishing for other species. Our analysis focused on variable costs and short-run decisions, because we were concerned primarily with decisions about whether to participate in the northern anchovy reduction fishery as a sideline activity rather than with decisions about whether to quit the wetfish fishery altogether.

A share system, described below, is used in the wetfish fishery to divide certain variable costs and revenues between boat owners and the crew; fixed costs, however, are paid by boat owners from their share of revenues. Fixed costs for the wetfish fleet tend to be modest because most boats are owned outright (mortgages are paid off) and boat owners consider hull insurance for boats with wooden hulls too expensive to purchase.

### *Opportunity Costs*

Most of the costs entailed in fishing or any business activity are tangible and readily quantified because they involve an exchange of money for goods and services. In contrast, opportunity costs are not an out-of-pocket expenditure but a measure of opportunities forgone in the course of making employment, business, and consumer decisions. The concept of opportunity cost reflects the reality that limited time and resources allow people to pursue economic opportunities only at the "cost" of forgoing alternatives (Ferris and Plourde 1982; Charles 1988). For boat owners, the opportunity cost of fishing is the income that they could expect to earn in an alternative business activity. For crew members, opportunity cost is the income that they could expect to earn in an alternative occupation.

The important point in connection with crew shares and opportunity costs is that crew members will tend to cease fishing and find other employment when crew shares fall below opportunity costs. Opportunity costs vary among fishermen, depending on the market value of their skills and how flexible they are about where they will work and what they will do for a living. Crew members who cherish fishing as a lifestyle may continue to participate when their apparent opportunity cost exceeds their earnings because they enjoy a "satisfaction bonus" from fishing that is sufficient compensation for forgone income (Smith 1981).

### *Types of Crew Members in the Wetfish Fleet*

"Traditional" wetfish fishermen come from the Italian-American and Yugoslav-American fishing community in San Pedro. The ethnic composition of crew members has changed in recent years: individuals from other (mainly Hispanic) ethnic backgrounds have been replacing traditional ethnic groups. Data for seven boats whose crew members belonged to the Fisherman and Allied Workers Union in San Pedro indicated that Hispanics ("nontraditional" wetfish fishermen) increased from 5% of total crew members in 1980 to 20% in 1990. Industry sources indicated that the Hispanic representation was even higher during 1990 on nonunion boats. According to boat owners and union personnel, many Hispanics employed in the fishery are recent immigrants to the USA who tend to have employment opportunities limited to low-paying jobs. For this reason, we consider the legal minimum wage ($\$4.25 \cdot h^{-1}$ in California during 1991) to be a reasonable estimate of the opportunity cost for nontraditional crew members.

TABLE 2.—Mathematical symbols used in the analysis. \$ = U.S. dollars.

| Symbol | Description and units |
|---|---|
| $b$ | Spawning biomass (1,000 tonnes) |
| $f$ | Catch rate (1,000 tonnes$\cdot$h$^{-1}$) |
| $p$ | Ex-vessel price (\$$\cdot$tonne$^{-1}$) |
| $R$ | Total revenue (\$$\cdot$h$^{-1}$) |
| $\alpha$ | Parameter used to relate biomass and catch rates |
| $\beta$ | Parameter used to relate biomass and catch rates |
| $C_t$ | Costs that depend on time spent fishing (\$$\cdot$h$^{-1}$) |
| $C_f$ | Costs that depend on catch rate (\$$\cdot$h$^{-1}$) |
| $C_g$ | Costs that depend on gross revenue (\$$\cdot$h$^{-1}$) |
| $\Phi$ | Price of fuel (\$$\cdot$L$^{-1}$) |
| $\pi$ | Landings tax for northern anchovy (\$$\cdot$tonne$^{-1}$) |
| $R$ | Gross revenue (\$$\cdot$h$^{-1}$) |
| $R_a$ | Adjusted revenue (\$$\cdot$h$^{-1}$), $R - C_f - C_g - C_t$ |
| $R_c$ | Crew member's share of adjusted revenue (\$$\cdot$person$^{-1}\cdot$h$^{-1}$) |
| EIV | Error-in-variables regression estimate for parameters |

Boat owners indicated during interviews that, whereas nontraditional crew members would likely be willing to fish for northern anchovy at a price of \$50$\cdot$tonne$^{-1}$, traditional crew members would not. Moreover, boat owners, who were almost all from traditional backgrounds, indicated that they were reluctant to fish with an exclusively nontraditional crew because, in their opinion, nontraditional crew members tend to be less experienced, communicating with them is more difficult, and they have a higher turnover rate than traditional fishermen. This reluctance was probably reinforced by cultural differences between traditional and other fishermen, and by familial ties that often exist between boat owners and traditional crew members.

Industry sources indicated that \$50$\cdot$tonne$^{-1}$ was the minimum price that would induce traditional crew members to participate in the reduction fishery. This assertion was supported by historical records indicating that reduction fishing virtually ceased when the ex-vessel price fell below \$50$\cdot$tonne$^{-1}$ (Table 1). We used the model described below to calculate hourly wages for crew members at ex-vessel prices of \$50$\cdot$tonne$^{-1}$ and, because interviews and our data indicated that \$50$\cdot$tonne$^{-1}$ was the critical price, we assumed that the result was an estimate of opportunity costs for traditional crew members in the wetfish fishery.

## Model

Our model, which was similar to that used by Perrin and Noetzel (1970), related crew shares to ex-vessel price, biomass, and catch rates for northern anchovy, and fuel price, landings tax, and miscellaneous costs. Vessels, fishing practices, and cost-sharing arrangements in the wetfish fishery have changed little during the last few years, so the model should remain useful until major changes occur in the fishery. With minor modifications, the model should be useful for species other than northern anchovy that are also harvested by the wetfish fleet (e.g., Pacific sardine). Mathematical symbols used in the model are summarized in Table 2.

### *Revenues*

Revenues (expressed on a per-hour basis) depend on catch rates and ex-vessel prices:

$$R = fp. \tag{1}$$

The relationship between catch rates and total biomass was assumed to be nonlinear:

$$f = \alpha b^{\beta}. \tag{2}$$

Substituting equation (2) into equation (1) gives revenues per hour as a function of ex-vessel prices and northern anchovy biomass:

$$R = \alpha b^{\beta} p. \tag{3}$$

We used an error-in-variables (EIV) regression analysis to obtain estimates of $\alpha = 0.38$ and $\beta = 0.39$ (Jacobson and Thomson 1992). An approximate 95% confidence interval for the EIV estimates was bounded by $\alpha = 3.95$ and $\beta = 0.03$, and by $\alpha = 0.05$ and $\beta = 0.71$.

The relationship between biomass and catch rates was assumed to be nonlinear because abundance is not the only factor that affects northern anchovy catch rates (Bannerot and Austin 1983, and references therein; Pacific Fishery Management Council 1983). The southern California reduction fishery operates in an area smaller than the range of the stock; thus, catch rates probably reflect abundance of northern anchovy in the area where the fleet operates but not total abundance over the range of the stock. Aerial fish spotters (pilots employed by commercial fishermen to locate schools of fish; see Squire 1972) are usually used to search for schools and direct the setting of nets; this approach reduces time spent searching by boats and increases catch rates. Trip limits on northern anchovy landings are often imposed by processors who are constrained by market orders and processing capacity. Finally, it is well known that, for schooling species such as northern anchovy, catch rates decline more slowly than abundance (Bannerot and Austin 1983). The effects of these problems on our analysis were minimized by using a nonlinear model (equation 2) for the relationship between catch rates and biomass and by not extrapolating beyond the range of data used to fit the model.

### *Costs*

The following operating costs affect crew shares in the northern anchovy fishery: (1) costs that depend on time spent at sea ($C_t$), (2) costs that depend on the catch rate ($C_f$), and (3) costs that depend on gross revenue ($C_g$). For convenience, these costs were expressed in units of dollars per hour at sea ($\$\cdot h^{-1}$).

Costs that vary with time at sea include fuel and ship-to-shore telephone expenses:

$$C_t = 143\Phi + 6.8; \tag{4}$$

143 $L\cdot h^{-1}$ was the average fuel consumption rate reported by fishermen during interviews. Mean ship-to-shore telephone expenses ($\$6.8\cdot h^{-1}$) were computed from mean cost per trip ($\$81\cdot trip^{-1}$, estimated from business records) and mean trip duration (12 h, estimated from logbook data).

Costs that depend on catch rate include a landings tax levied by the state of California and two special assessments (patrol fund and wetfish assessment) levied by the industry itself. The patrol fund supports an employee who observes unloading of fish to ensure that boat owners and crew are paid for all fish actually landed. The wetfish assessment is used to support legislative and management programs. According to business records, the costs were $\$1.82\cdot tonne^{-1}$ for the patrol fund and $\$0.23\cdot tonne^{-1}$ for the wetfish assessment.

In the model, costs that depend on catch rate were

$$C_f = (\pi + 2.05)f; \tag{5}$$

$\$2.05\cdot tonne^{-1}$ was the sum of the special assessments. To correspond to state laws, $\pi$ varied with $p$ (ex-vessel price):

$$\pi = \$1.32\cdot tonne^{-1} \quad \text{when } p < \$45.40\cdot tonne^{-1}; \tag{6}$$

$$\pi = \$2.89\cdot tonne^{-1} \quad \text{when } p \geq \$45.40\cdot tonne^{-1}.$$

Costs that depend on gross revenues include payments to fish spotters and pension benefits for the crew, which according to business records were 5 and 2% of gross revenues, respectively. Thus, these costs were

$$C_g = 0.07\, fp. \tag{7}$$

### *Hourly Wages for Crew Members*

The share system used in the wetfish fishery splits total adjusted revenues (total revenues minus costs described above) between boat owners and crew. Total adjusted revenues ($R_a$) were calculated:

$$R_a = R - C_t - C_f - C_g. \tag{8}$$

Business records and interviews indicated that, on average during 1990, vessel owners received 48% of total adjusted revenues and crew members received 52%; there was some minor variability from boat to boat. According to industry sources, these proportions have changed little over time. According to data obtained from the California Department of Fish and Game, average crew size in the wetfish fleet (including the skipper) was 8.9 crew members per boat. The hourly wage (gross wage before deductions for groceries, taxes, and union dues) per crew member ($\$\cdot person^{-1}\cdot h^{-1}$) was

$$R_c = 0.52\, R_a/8.9. \tag{9}$$

The following equation results when equations (2)–(8) are substituted for terms in equation (9):

$$R_c = 0.058\alpha b^{\beta}(0.930p - 2.050 - \pi) - 8.355\Phi - 0.397. \tag{10}$$

Hence, the hourly wage per crew member ($R_c$) was a function of northern anchovy biomass, ex-vessel price, landings tax rate, diesel fuel price, and parameters $\alpha$ and $\beta$.

We used equation (10) to compute average hourly wages for crew members at northern anchovy biomass levels of 300,000–1,700,000 tonnes, ex-vessel prices of $\$30$–$100\cdot$tonne, and diesel fuel prices of \$0.125, \$0.25, and \$0.375 per liter (Table 3). The ex-vessel prices and northern anchovy biomass levels used in our calculations covered the range of historical data. Biomass estimates for northern anchovy during 1964–1990 ranged from 306,000 to 1,800,000 tonnes; the first quartile was at 401,000 tonnes, the median was at 529,000 tonnes, and third quartile was at 852,000 tonnes (Jacobson and Lo 1990). The lower limit of the range used for biomass levels corresponded to management regulations, because reduction fishing is not permitted at spawning biomass levels lower than 300,000 tonnes. The range of fuel prices (\$0.25 ± 50%) was centered around the average spot price for diesel fuel sold to wetfish fishermen by a distributor in San Pedro during 1990 (D. Squires, Southwest Fisheries Science Center, personal communication).

TABLE 3.—Hourly wages for crew members ($$\$ \cdot h^{-1}$$) estimated under various assumptions about ex-vessel price, northern anchovy biomass, and the price of fuel. $ = U.S. dollars.

| Biomass (1,000 tonnes) | Ex-vessel price (per tonne landed): | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | $30 | $40 | $50 | $60 | $70 | $80 | $90 | $100 |
| | | | **Fuel price = $0.125·L$^{-1}$** | | | | | |
| 300 | 3.60 | 5.52 | 7.11 | 9.02 | 10.93 | 12.85 | 14.76 | 16.67 |
| 500 | 4.72 | 7.05 | 8.99 | 11.33 | 13.66 | 16.00 | 18.33 | 20.66 |
| 700 | 5.58 | 8.24 | 10.46 | 13.12 | 15.78 | 18.44 | 21.10 | 23.76 |
| 900 | 6.30 | 9.24 | 11.68 | 14.62 | 17.55 | 20.49 | 23.42 | 26.36 |
| 1,100 | 6.93 | 10.11 | 12.75 | 15.92 | 19.10 | 22.27 | 25.45 | 28.62 |
| 1,300 | 7.50 | 10.89 | 13.70 | 17.09 | 20.48 | 23.87 | 27.26 | 30.65 |
| 1,500 | 8.01 | 11.59 | 14.57 | 18.16 | 21.74 | 25.32 | 28.91 | 32.49 |
| 1,700 | 8.48 | 12.25 | 15.37 | 19.14 | 22.90 | 26.66 | 30.42 | 34.19 |
| | | | **Fuel price = $0.25·L$^{-1}$** | | | | | |
| 300 | 2.56 | 4.47 | 6.06 | 7.98 | 9.89 | 11.80 | 13.71 | 15.63 |
| 500 | 3.67 | 6.01 | 7.95 | 10.28 | 12.62 | 14.95 | 17.29 | 19.62 |
| 700 | 4.54 | 7.20 | 9.41 | 12.07 | 14.73 | 17.40 | 20.06 | 22.72 |
| 900 | 5.26 | 8.19 | 10.64 | 13.57 | 16.51 | 19.44 | 22.38 | 25.32 |
| 1,100 | 5.89 | 9.06 | 11.70 | 14.88 | 18.05 | 21.23 | 24.40 | 27.58 |
| 1,300 | 6.45 | 9.84 | 12.66 | 16.05 | 19.44 | 22.83 | 26.21 | 29.60 |
| 1,500 | 6.97 | 10.55 | 13.53 | 17.11 | 20.70 | 24.28 | 27.86 | 31.44 |
| 1,700 | 7.44 | 11.20 | 14.33 | 18.09 | 21.85 | 25.62 | 29.38 | 33.14 |
| | | | **Fuel price = $0.375·L$^{-1}$** | | | | | |
| 300 | 1.52 | 3.43 | 5.02 | 6.93 | 8.84 | 10.76 | 12.67 | 14.58 |
| 500 | 2.63 | 4.96 | 6.90 | 9.24 | 11.57 | 13.91 | 16.24 | 18.58 |
| 700 | 3.49 | 6.15 | 8.37 | 11.03 | 13.69 | 16.35 | 19.01 | 21.68 |
| 900 | 4.21 | 7.15 | 9.59 | 12.53 | 15.46 | 18.40 | 21.34 | 24.27 |
| 1,100 | 4.84 | 8.02 | 10.66 | 13.83 | 17.01 | 20.18 | 23.36 | 26.53 |
| 1,300 | 5.41 | 8.80 | 11.62 | 15.00 | 18.39 | 21.78 | 25.17 | 28.56 |
| 1,500 | 5.92 | 9.50 | 12.48 | 16.07 | 19.65 | 23.23 | 26.82 | 30.40 |
| 1,700 | 6.39 | 10.16 | 13.29 | 17.05 | 20.81 | 24.57 | 28.34 | 32.10 |

## Results

Hourly wages for crew members (Table 3) increased over the range of ex-vessel prices ($30–100·tonne$^{-1}$) by about 400% on average (400% is the mean increase at each fuel price and biomass level in Table 3). Hourly wages increased over the range of biomass levels (300,000–1,700,000 tonnes) by about 140% on average. Hourly wages decreased over the range of fuel prices ($0.125–0.375·L$^{-1}$) by about 22% on average. The proportional effect of ex-vessel prices was greatest at high fuel prices and low northern anchovy biomass levels. The proportional effect of northern anchovy biomass was greatest at high fuel prices and low ex-vessel prices. The proportional effect of fuel prices was greatest at low ex-vessel prices and low northern anchovy biomass levels.

Hourly wages for crew members were positive even at the lowest biomass levels, lowest ex-vessel prices, and highest fuel prices (Table 3), indicating that ex-vessel revenues were sufficient to cover variable costs shared by boat owner and crew in reduction fishing under a wide variety of fishery conditions. The important conclusion from these results was that inability to cover variable costs was apparently not a factor in the decline of the northern anchovy reduction fishery.

As discussed earlier, crew members' hourly wages associated with the prevailing fuel price ($0.25·L$^{-1}$) and minimum acceptable ex-vessel price for northern anchovy fishing ($50·tonne$^{-1}$) were reasonable estimates of opportunity costs for traditional fishermen. Results from the model (Table 3) indicated that opportunity costs for traditional fishermen were in the range of $6.06–14.33·h$^{-1}$. These estimates for traditional fishermen were considerably higher than our estimate of opportunity cost for nontraditional fishermen ($4.25·h$^{-1}$).

Hourly earnings in excess of opportunity cost for nontraditional fishermen ($4.25·h$^{-1}$) can be expected at a wide range of biomass levels and fuel costs, even when ex-vessel prices are as low as $30·tonne$^{-1}$ (Table 3). Thus, the results from our model are consistent with information from boat owners indicating that nontraditional fishermen would be willing to fish for northern anchovy in

TABLE 4.—Hourly wages for crew members ($·h$^{-1}$) estimated under the assumption of ex-vessel prices of $30, $40, and $50 per tonne landed, a fuel price of $0.25·L$^{-1}$, the historical range of northern anchovy biomass, and an approximate 95% confidence interval for estimates of $\alpha$ and $\beta$. The middle estimates ($\alpha = 0.38$, $\beta = 0.39$) are "best estimates" from an EIV regression. The other two sets of estimates ($\alpha = 3.95$, $\beta = 0.03$; and $\alpha = 0.05$, $\beta = 0.71$) bound the confidence interval. $ = U.S. dollars.

| Biomass (1,000 tonnes) | $\alpha = 3.95$, $\beta = 0.03$, and ex-vessel price is: | | | $\alpha = 0.38$, $\beta = 0.39$, and ex-vessel price is: | | | $\alpha = 0.05$, $\beta = 0.71$, and ex-vessel price is: | | |
|---|---|---|---|---|---|---|---|---|---|
| | $30 | $40 | $50 | $30 | $40 | $50 | $30 | $40 | $50 |
| 300 | 4.24 | 6.79 | 8.92 | 2.56 | 4.47 | 6.06 | 1.63 | 3.19 | 4.49 |
| 500 | 4.35 | 6.94 | 9.09 | 3.67 | 6.01 | 7.95 | 3.43 | 5.68 | 7.54 |
| 700 | 4.42 | 7.03 | 9.21 | 4.54 | 7.20 | 9.41 | 5.03 | 7.88 | 10.25 |
| 900 | 4.47 | 7.11 | 9.30 | 5.26 | 8.19 | 10.64 | 6.50 | 9.91 | 12.74 |
| 1,100 | 4.51 | 7.16 | 9.37 | 5.89 | 9.06 | 11.70 | 7.88 | 11.80 | 15.07 |
| 1,300 | 4.55 | 7.21 | 9.43 | 6.45 | 9.84 | 12.66 | 9.18 | 13.60 | 17.28 |
| 1,500 | 4.58 | 7.25 | 9.48 | 6.97 | 10.55 | 13.53 | 10.43 | 15.32 | 19.39 |
| 1,700 | 4.60 | 7.29 | 9.52 | 7.44 | 11.20 | 14.33 | 11.63 | 16.98 | 21.43 |

the reduction fishery at prices less than $50·tonne$^{-1}$ but traditional fishermen would not.

To evaluate the potential effects of uncertainty about the relationship between biomass and catch rates in equation (2), we calculated crew members' hourly wages for values of $\alpha$ and $\beta$ corresponding to the 95% confidence interval around our estimates from the EIV regression, for ex-vessel prices of $30, $40, and $50 per tonne, for the range of northern anchovy biomass levels, and for a fuel price of $0.25·L$^{-1}$ (Table 4).

Results obtained with different parameter values were essentially the same as those obtained with EIV estimates (Table 4). The opportunity cost of traditional fishermen at the approximate median biomass level of northern anchovy (500,000 tonnes), for example, was estimated to be $8·h$^{-1}$ with EIV parameter estimates and about $7.50–9.00·h$^{-1}$ over the range of alternative parameter values considered. Hourly wages for crew members exceeded the opportunity cost of nontraditional fishermen ($4.25·h$^{-1}$) over a wide range of biomass levels and at ex-vessel prices as low as $30·tonne$^{-1}$ (Table 4).

## Discussion

The results of our analysis reflect current biological, economic, and sociological conditions in the wetfish fishery. Relationships involving opportunity costs will probably change as conditions in the fishery change. In the long run, for example, a significant decline in abundance or ex-vessel prices for wetfish species other than northern anchovy could result in a sizeable increase in the minimum acceptable price for northern anchovy, because revenues from fishing for other species could not be used to meet fixed costs. A northern anchovy reduction fishery might be reestablished, even at low ex-vessel prices and low northern anchovy biomass levels, if boat owners are willing to work with an exclusively nontraditional crew who would accept earnings at the minimum wage level or if boats are purchased by people who are comfortable working with nontraditional crew members. Thus, changes in ethnic backgrounds of boat owners and crews may have important effects on the wetfish fishery.

### *Management Applications*

The northern anchovy fishery is managed on the basis of a formula that links the catch quota for reduction fishing to the level of spawning biomass (Pacific Fishery Management Council 1983, 1990). The best, but most expensive, estimates of spawning biomass for northern anchovy are obtained with the egg production method described in Lasker (1985). As an alternative, less-accurate and less-expensive approaches are used (Methot 1989; Jacobson and Lo 1990). The egg production method has not been used to collect data in recent years because of inactivity in the U.S. northern anchovy reduction fishery and the expense involved with the method. Our analysis sheds light on reasons for inactivity in the fishery and should help managers to anticipate increased harvest levels, due to increased ex-vessel prices or changes in the ethnic composition of crew members and boat owners, and the need to obtain more precise biomass estimates by the egg production method.

The Pacific Fishery Management Council is developing a federal fishery management plan for coastal pelagic fisheries on the west coast of the USA. The new plan will address management of fisheries for chub mackerel, jack mackerel, Pacific sardine, and northern anchovy. In development of the plan, the council is responsible for considering socioeconomic, as well as biological, information (Magnuson Fishery Conservation and Management Act, Public Law 94-265). Our study provides useful information about opportunity costs and variable costs that are important, but usually neglected, elements in socioeconomic analyses used for fishery management.

### Acknowledgments

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# VENTRICULAR AND ARTERIAL DYNAMICS OF ANAESTHETISED AND SWIMMING TUNA

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## Summary

Cardiovascular dynamics of tuna have been investigated by recording blood pressures and flows in the central circulation of both anaesthetised and swimming individuals. In anaesthetised fish ($N$=5), heart rate averaged 112±21 beats min$^{-1}$ (mean ± S.E.) and stroke volume was 0.67±0.24 ml kg$^{-1}$ when normoxic water flowed over the gills. Ventricular diastolic pressure was zero until atrial contraction filled the ventricle. Ventral aortic pressures were high (mean 12.08±1.15 kPa), and blood flow was continuous in the ventral aorta throughout diastole. Dorsal aortic pressure (mean 6.3±1.28 kPa; $N$=4) and flow were both pulsatile. Pressure pulsatility (pulse pressure as a proportion of mean pressure) was about one-quarter of flow pulsatility, indicating considerable compliance in the dorsal aortic circulation. Total peripheral resistance averaged 0.17±0.4 kPa ml$^{-1}$ kg$^{-1}$ min$^{-1}$ of which gill resistance averaged 48±15 % ($N$=4). For the ventral aorta, impedance modulus fell markedly from the mean value and then declined more gradually towards zero with increasing harmonic frequencies. Impedance phase was negative (−0.8 to −1.1 rad) meaning that flow leads pressure at all harmonics. In swimming yellowfin tuna ($N$=5), heart rate averaged 108.8±12.1 beats min$^{-1}$ and mean ventral and dorsal aortic pressures were 11.6±0.5 and 6.8±1.2 kPa, respectively, so gill resistance was 42 % of total peripheral resistance. Average stroke volume in three swimming kawakawa was 0.54±0.2 ml kg$^{-1}$ at a mean heart rate of 128±48 beats min$^{-1}$. Data from swimming fish were within the range obtained from anaesthetised tuna. A simple model of the fish circulation consisting of two sets of compliant and resistive elements coupled in series (a second-order $RC$ network) gave reasonable predictions of arterial pressure–flow relationships. Hence, we conclude that a 'Windkessel' dominates central cardiovascular dynamics of tuna despite heart rates and blood pressures that fall in the mammalian range.

## Introduction

A Windkessel model describes the arterial system in terms of a simple elastic reservoir

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(the lumped compliance of the major arteries) which feeds the terminal resistance vessels (Burkhoff *et al.* 1988). The electrical analogue of the Windkessel is an *RC* network (where *R* is resistance and *C* is capacitance). The cardiovascular system of fish is usually described as two '*RC* networks' in series (a second-order *RC* network), supplied by a single signal generator (the heart) (Satchell, 1971). The lumped, but separate, compliances of the ventral and dorsal aortae feed resistance vessels of the gills and systemic vasculature, respectively. The ventral aorta is short, and gill resistance is usually about one-quarter of total peripheral resistance (Holeton and Randall, 1967; Satchell, 1971; Kiceniuk and Jones, 1977; Lai *et al.* 1987). However, compliance of the ventricular outflow tract is enhanced by a highly elastic segment, the bulbus arteriosus, contained within the pericardium (Satchell, 1971; Licht and Harris, 1973; Priede, 1976; Farrell, 1979; Bushnell *et al.* 1992).

Pressure and flow relationships are usually analysed using a hydraulic equivalent (pressure=flow×resistance) of Ohm's law for direct current (d.c.) electrical circuits. However, both pressure and flow are pulsatile, and haemodynamic analysis is better served by considering not only the mean values of pressure and flow but also the sine-wave harmonics of the pulsatile waveforms. The harmonics are obtained from a Fourier analysis of the original pressure and flow waveforms (McDonald, 1974; Jones, 1991). The quotient obtained by dividing oscillatory pressure by oscillatory flow is termed impedance modulus, and the phase angle between any pair of harmonics of pressure and flow of the same frequency is termed impedance phase. For a Windkessel, impedance modulus falls markedly from the d.c. value (peripheral resistance) at the first harmonic and then decreases successively towards zero with increasing harmonics. Peak flow occurs before peak pressure so the phase angle between pressure and flow is negative at all harmonics. In birds and mammals, however, oscillations in both modulus and phase occur with increasing harmonic frequencies (Langille and Jones, 1975; Milnor, 1979). The oscillations are caused by interactions between incident waves, generated by cardiac contraction, and reflected waves from the peripheral vasculature. These wave transmission effects are obviously not observed in a Windkessel formulation because one of the fundamental tenets of the Windkessel theory is that changes generated by cardiac contraction occur simultaneously throughout the arterial system (McDonald, 1974; Jones, 1991).

Heart rates in most fish are low, so wave transmission time from the bulbus to the gills (the first Windkessel) will be a negligible fraction of the cardiac cycle. Hence, wave transmission effects in this part of the circulation should be negligible. However, heart rates of tuna in normoxic water and at high temperatures (13–25 °C) may reach 260 beats $\min^{-1}$ (Kanwisher *et al.* 1974; Brill, 1987), which are far higher than those achieved by other active teleosts such as salmon and trout (Smith *et al.* 1967; Kiceniuk and Jones, 1977). It is possible that, at high repetition rates, wave transmission phenomena, such as the oscillating pattern of arterial impedance seen in birds and mammals, could influence arterial haemodynamics in fish (O'Rourke, 1967; O'Rourke and Taylor, 1967; McDonald, 1974; Milnor, 1979).

Consequently, in order to investigate arterial haemodynamics we have made pressure recordings in the heart, and pressure and flow recordings in the ventral and dorsal aortae, of anaesthetised tuna to examine pressure–flow relationships. We also wanted to know how well our data, obtained from anaesthetised fish on an operating table, would relate to fish swimming in the holding tanks (Jones *et al.* 1986). Our equipment did not allow high-fidelity recordings of pressure and flow from swimming fish. Nevertheless, we felt that these data would be useful, even if only to put our haemodynamic study in a more realistic context. Finally, a Windkessel model consisting of two sets of compliant and resistive elements coupled in series (Satchell, 1971; Jones *et al.* 1974; Langille *et al.* 1983) has been used to predict pressure and flow relationships in the ventral aorta, which were compared with measured values.

## Materials and methods

The experiments were performed on six kawakawa (*Euthynnus affinis* Cantor) and twelve yellowfin tuna (*Thunnus albacares* Bonnaterre). The fish were held in large outdoor tanks at the National Marine Fisheries Service Kewalo Research Facility in Honolulu, HI, USA. Water temperature in the holding and working tanks was 25 °C. Fish were trapped and anaesthetised in the holding tanks as described previously (Jones *et al.* 1986) and then quickly moved to an operating table, where they were suspended in a chamois-leather-lined cradle. Anaesthesia was maintained by pumping aerated sea water containing 1:1200 w/v MS-222 over the gills. After instrumentation, the fish was removed from the operating cradle and held upright in a large tank under light anaesthesia, maintained by periodic injections of Saffan ($3\,\mathrm{mg\,kg^{-1}}$ intra-arterially; Glaxovet, Montreal, PQ, Canada). At this level of anaesthesia, the fish made slow swimming movements. Gill irrigation was achieved by pumping water into the mouth through a soft rubber hose.

### *Studies on cardiovascular dynamics*

### *Restrained fish*

An anaesthetised fish was suspended in the chamois-leather-lined cradle ventral side up. An incision was made in the midline, in front of the bulbus arteriosus. Muscles and blood vessels were parted by blunt dissection and one of two types of flow transducer was placed around the ventral aorta. The transducer was connected to a Biotronix BL 610 pulsed logic electromagnetic flowmeter (Biotronix Inc, Silver Spring, MD) or a Crystal Biotech pulsed Doppler flowmeter (Crystal Biotech, Holliston, MA, USA) as appropriate. Large venous sinuses surrounding the dorsal aorta prevented a direct approach to that vessel. Instead, flow was monitored through the roof of the buccal cavity using a specially modified surface probe (paediatric probe) connected to a portable, battery-operated, Parks Medical Systems continuous Doppler flowmeter (Portland, OR, USA). The probe was sutured to the roof of the mouth, over the dorsal vessel, just in front of the oesophageal sphincter. Sutures were passed through holes bored in each corner of the probe. To restrict any movement, the probe was also glued to the roof of the mouth with Histoacryl tissue cement (B. Braun, Germany). At the conclusion of measurements the animal was killed by anaesthetic overdose (Pentothal, intra-arterially; Abbott Labs, IL, USA) and, after exposure and cannulation of the ventral and dorsal aortae, the flow probes were calibrated *in situ* using tuna blood pumped at three or more different flow rates through the vessels by a Harvard infusion pump (Harvard Apparatus Company Inc, Millis, MA, USA). A regression line constrained to go through zero was fitted to the data on a plot of flow (ml $\mathrm{min}^{-1}$) *versus* flowmeter output. The flow recording was deemed acceptable if the three calibration values were within ±5 % of the regression line. This stricture led to the rejection of two dorsal aortic flow recordings made in anaesthetised fish and three cardiac output recordings made in swimming fish. However, in data used for harmonic analysis, the pulsed Doppler flow probe was calibrated by injecting a known volume of blood into the ventral aorta during diastole when the heart rate was slowed by passing deoxygenated water over the gills. Volumes injected varied from 0.5 to 2 ml. The flowmeter signal was integrated over time to give volume flow. Up to 10 injections were made in an animal and regression lines were fitted to the data on a plot of volume flow *versus* flowmeter output.

Angiocaths (nos 18, 20 or 22; 38 or 50 mm long) were inserted into the ventricle, bulbus arteriosus, ventral aorta and dorsal aorta under manometric guide, as described previously (Jones *et al.* 1986). Each angiocath was connected to a Bio-Tek BT 70 pressure transducer (Bio-Tec, Pasadena, CA, USA) using polyethylene tubing of various lengths and bores filled with heparinized saline (50 i.u. $\mathrm{ml}^{-1}$). The frequency response of the manometric system was between 35 and 60 Hz, with damping between 0.12 and 0.4 of critical damping when subjected to pop-tests before and after recordings (Jones, 1970). Manometers with high-frequency responses (60 Hz) and low damping (0.12–0.2 of critical) were used to obtain pressure data for Fourier analysis. The polyethylene tubing was sewn into position close to the incision and near the dorsal fin.

The fish was turned upright, removed from the cradle and suspended in a large tank. Pressures and flows were recorded at resting heart rates, at reduced heart rates, caused either by stopping water flow or by passing deoxygenated water over the gills, and after stimulation of cardiac function by injection of 0.3 ml $\mathrm{kg}^{-1}$ of phenylephrine (intra-arterially).

### *Swimming fish*

The dorsal and ventral aortae of five yellowfin tuna were cannulated as described previously (Jones *et al.* 1986) and, after recovery from anaesthesia, fish were allowed to swim laps in a doughnut-shaped tank (17.1 m internal and 17.9 m external diameter). Dorsal and ventral aortic pressures were measured using pressure manometers connected to hand-held strain gauge bridge amplifiers. These amplifiers were connected by long cables to a two-channel pen recorder. One of us, holding the manometers and amplifiers, ran around the tank keeping pace with the fish while the others endeavoured to keep the electrical connections to the chart recorder untwisted and out of the water.

Ventral aortic flow was recorded in six kawakawa using the modified surface probe (described above) connected to the Parks Medical Systems continuous Doppler flowmeter. The anaesthetised fish was placed in the operating cradle and a flexible plastic spatula was used to reflect the gills and expose the ventral aorta. The surface probe was placed on the skin over the aorta, sutured at each corner, and fixed in position with tissue cement. The fish was placed in the doughnut-shaped tank and artificially ventilated until recovery was complete. Zero flow was defined as diastolic flowmeter output during extreme bradycardia induced by stopping artificial ventilation. One of us, carrying the flowmeter, accompanied the fish while it swam around the tank. At the end of the recording period the flowmeter was calibrated by passing blood at three or more known rates of flow through the ventral aorta using the Harvard pump attached to a cannula tied into the bulbus arteriosus. The flowmeter was calibrated successfully in three of the six tuna.

### *Data collection and analysis*

All pressures and flows were recorded on Gould two- or six-channel ink recorders (Gould Instruments, Cleveland, OH, USA) writing on rectilinear coordinates. Vascular impedance at the input to the ventral aorta was determined in three yellowfin tuna. Approximately 40 pairs of ventral aortic pressures and flows were digitized into 256 or 512 points, using a data collection system (Dianechart, Rockaway, NJ, USA), and the data were stored directly on disk. Fourier analysis of the pressure and flow signals was carried out using a computer running SYSTAT software (Systat, Inc; Evanston, IL, USA). The quotient of pressure divided by flow (impedance modulus) and the phase difference between pressure and flow were obtained for the first five harmonics. The frequency response of the flowmeter was 66 kHz. The frequency response of the manometers was 4–5 times the highest harmonic analysed. We made no corrections for amplitude or phase distortions introduced by the manometer. Peak, mean and minimum values for pressure and flow, as well as heart rate and temporal events of the cardiac cycle (i.e. time of atrial contraction, diastolic period, etc.) were obtained from recorder charts digitized using SIGMASCAN (Jandel Scientific, Corte Madera, CA, USA). Maximum rate of pressure change ($dP/dt$) during ventricular systole was obtained manually by drawing a tangent to the rising phase of the pressure curve on the recorder chart. Pressure and flow traces were superimposed, with respect to time, using SIGMAPLOT.

Stroke volume ($Q_S$) was obtained by dividing heart rate ($f_H$) into cardiac output ($\dot{Q}b$). Total peripheral resistance ($R_{TOT}$) was obtained by dividing $\dot{Q}b$ into mean ventral aortic pressure ($P_{VA}$). Systemic resistance $R_S$ was obtained by dividing $\dot{Q}b$ (or in one case dorsal aortic flow, $\dot{Q}_{DA}$, into mean dorsal aortic pressure ($P_{DA}$). Gill resistance ($R_G$) was obtained by subtracting $R_S$ from $R_{TOT}$. In the text, mean values are given accompanied by the standard error of the mean.

## Results

### *Cardiovascular dynamics*

#### *Restrained fish*

In normoxic yellowfin tuna, $f_H$ varied from 86 to 139 beats min$^{-1}$ (mean 112±21 beats min$^{-1}$) (Table 1). During ventilation with deoxygentated water, $f_H$ could fall as low as 10 beats min$^{-1}$, although measurements were not made at heart rates of less than 60 beats min$^{-1}$ because cardiovascular function did not appear to be stable at very low $f_H$. Changes in $f_H$ induced by hypoxia were not accompanied by large variations in

Table 1. *Cardiovascular variables recorded from anaesthetised yellowfin tuna*

|  |  | Fish 2 |  |  |  | Fish 5 |  |
|---|---|---|---|---|---|---|---|
|  | Fish 1 |  |  | Fish 3 | Fish 4 |  |  |
|  | Normoxia | Hypoxia | Normoxia | Normoxia | Normoxia | Hypoxia | Normoxia |
| Mass (kg) | 0.93 | 1.68 | 1.68 | 1.32 | 1.01 | 2.08 | 2.08 |
| Heart rate (beats min$^{-1}$) | 139 | 71 | 107 | 101 | 86 | 60 | 127 |
| Cardiac interval (ms) | 431 | 844 | 560 | 594 | 694 | 1009 | 472 |
| Ventricle |  |  |  |  |  |  |  |
| Systolic pressure (kPa) | 12.8 | 15.2 | 18.5 | – | 18.9 | – | – |
| Systolic interval (ms) | 242 | 266 | 270 | – | 273 | – | – |
| Diastolic pressure after atrial contraction (kPa) | 0.24 | 0.15 | 0.6 | – | 0.76 | – | – |
| d$P$/d$t$ (kPa s$^{-1}$) | 344 | 464 | 716 | 405 | – | – | – |
| Cardiac output (ml min$^{-1}$ kg$^{-1}$) | 79.6 | 47.5 | 95.0 | 49.1 | 81.8 | 44.0 | 53.8 |
| Stroke volume (ml kg$^{-1}$) | 0.57 | 0.67 | 0.89 | 0.49 | 0.95 | 0.75 | 0.43 |
| Ventral aorta |  |  |  |  |  |  |  |
| Systolic pressure (kPa) | 12.4 | 14.8 | 19.4 | 14.8 | 17.9 | 10.8 | 10.5 |
| Diastolic pressure (kPa) | 9.4 | 7.9 | 13.1 | 10.0 | 11.8 | 5.4 | 7.6 |
| Mean pressure (kPa) | 10.4 | 9.8 | 15.5 | 11.6 | 13.8 | 7.7 | 9.1 |
| % Pressure pulsatility (pulse/mean) | 29 | 70 | 41 | 42 | 44 | 70 | 32 |
| Peak flow (ml min$^{-1}$) | 142 | 226 | 232 | 189 | 156 | 377 | 280 |
| Minimum flow (ml min$^{-1}$) | 50.0 | 13.9 | 151.0 | 18.5 | 47.2 | 5.9 | 28.5 |
| % Flow pulsatility (pulse/mean) | 125 | 265 | 50 | 263 | 132 | 405 | 224 |
| Dorsal aorta |  |  |  |  |  |  |  |
| Systolic pressure (kPa) | – | 8.9 | 11.3 | 6.1 | – | 4.2 | 4.3 |
| Diastolic pressure (kPa) | – | 6.6 | 9.3 | 5.0 | – | 2.9 | 3.8 |
| Mean pressure (kPa) | – | 7.4 | 10.0 | 5.4 | 5.7 | 3.3 | 4.1 |
| % Pressure pulsatility | – | 31 | 20 | 20 | – | 40 | 12 |
| Peak flow (ml min$^{-1}$) | – | – | – | – | – | 81.6 | 92.5 |
| Minimum flow (ml min$^{-1}$) | – | – | – | – | – | 10.2 | 44.2 |
| Mean flow (ml min$^{-1}$ kg$^{-1}$) | – | – | – | – | – | 23.6 | 36.7 |
| % Flow pulsatility | – | – | – | – | – | 146 | 63 |
| Resistance |  |  |  |  |  |  |  |
| Total peripheral resistance (kPa ml$^{-1}$ kg$^{-1}$ min$^{-1}$) | 0.13 | 0.21 | 0.16 | 0.24 | 0.17 | 0.17 | 0.17 |
| Gill resistance (kPa ml$^{-1}$ kg$^{-1}$ min$^{-1}$) | – | 0.05 | 0.04 | 0.13 | 0.10 | 0.08 | 0.09 |
| Systemic resistance (kPa ml$^{-1}$ kg$^{-1}$ min$^{-1}$) | – | 0.16 | 0.11 | 0.11 | 0.07 | 0.07<br>(0.14)* | 0.08<br>(0.11)* |

During normoxia, water $P_{O_2}$ was 11–11.5 kPa and during hypoxia it was 3.75–5.25 kPa.
Ventilation volume was 6 l min$^{-1}$.

*Figures for systemic resistance in parentheses were calculated using dorsal aortic flow measured behind the gills, and therefore they do not include the vascular resistance of the head.

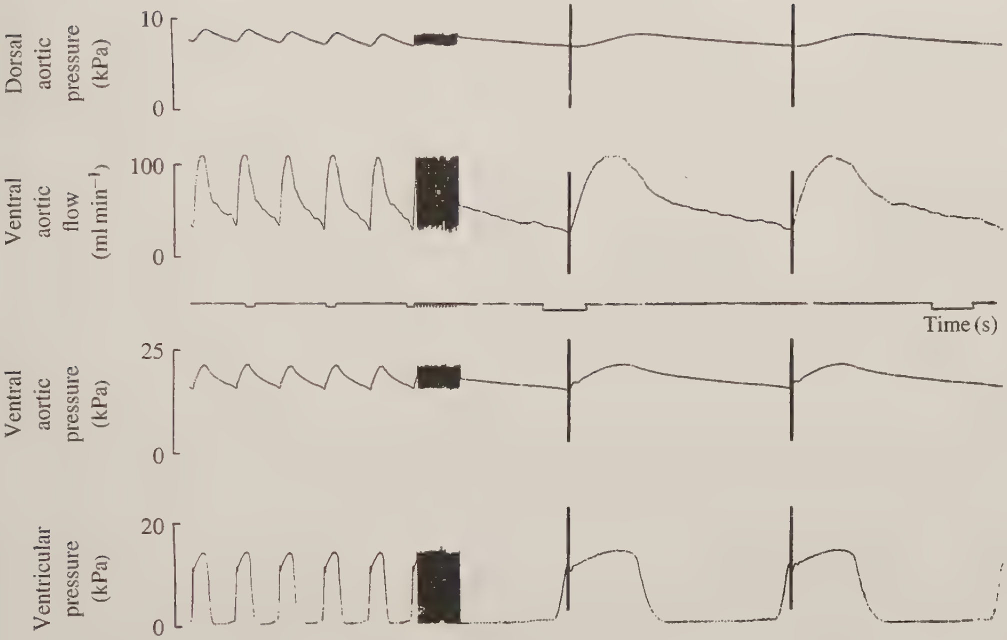

Fig. 1. Pressures and flow in the central circulation of a yellowfin tuna. Traces from top to bottom: dorsal aortic pressure, ventral aortic flow, time, ventral aortic pressure and ventricular pressure. The vertical lines link coincident points in time on pressure and flow traces. Note the changes in time base during the record.

either $P_{\mathrm{VA}}$ or $P_{\mathrm{DA}}$. $Q_{\mathrm{S}}$ averaged 0.67±0.24 ml kg$^{-1}$ in normoxic tuna and did not change consistently when heart rate changed. $Q_{\mathrm{S}}$ was reduced at low $f_{\mathrm{H}}$ in one fish but increased, compared with normoxic values, in another (Table 1).

Ventricular diastolic pressures were close to zero. Atrial contraction, which occurred some 70–90 ms before ventricular systole, increased ventricular pressure by between 0.15 and 0.76 kPa. During systole, ventricular pressure generation ($\mathrm{d}P/\mathrm{d}t$) attained remarkable rates of 344–716 kPa s$^{-1}$ (mean 482±163 kPa s$^{-1}$, $N$=4; Table 1). The rapid phase of pressure generation ceased when the bulbo-ventricular valves opened and both pressure and flow started in the ventral aorta (Fig. 1). $P_{\mathrm{VA}}$ was high (mean 12.08±1.15 kPa) and followed ventricular pressure during the ejection phase, but diverged soon after peak systole (see Fig. 3).

The length of the ejection phase averaged 263±14 ms ($N$=4) and bore a positive relationship to $Q_{\mathrm{S}}$. This relationship was most clearly seen after arterial phenylephrine injection: the ejection phase increased by 50 % and $Q_{\mathrm{S}}$ increased by 30 %. Peak ventral aortic flow occurred before peak pressure (Figs 1 and 2). The shape of the ventral aortic flow pulse was variable (Figs 1, 2, 3). Flow declined slowly in the ventral aorta after systole, although even at heart rates of 60 beats min$^{-1}$, zero flow was sometimes not reached by the end of diastole (Fig. 2). The flow pulsatility (pulse flow as a proportion of mean flow) in the ventral aorta was 4.3±1.0 times the pressure pulsatility (pulse pressure

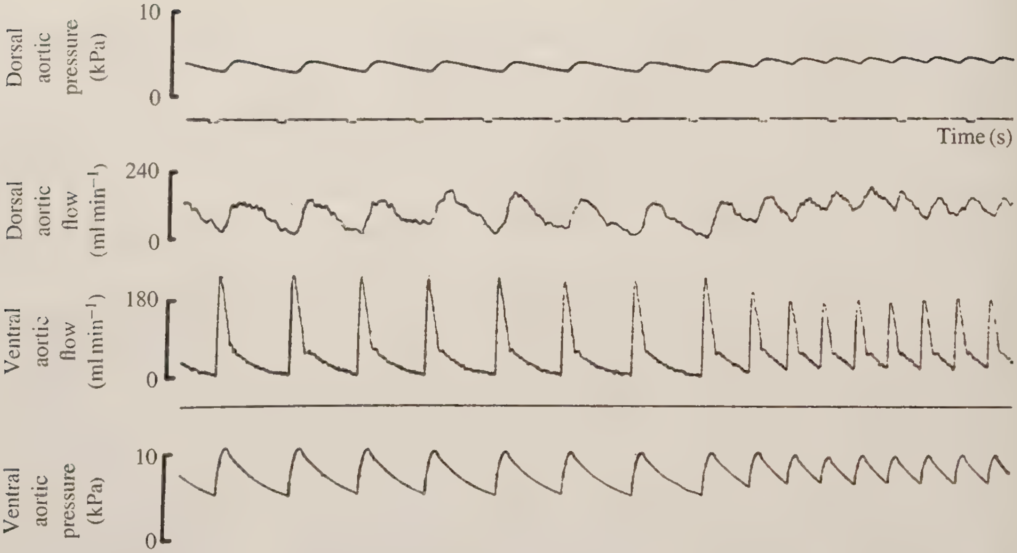

Fig. 2. Pressures and flows in the ventral and dorsal aortae of a yellowfin tuna. The low heart rate during the first 7 s was caused by passing hypoxic water over the gills.

as a proportion of mean pressure) during normoxia (Table 1). Mean $P_{DA}$ (6.3±1.28 kPa) was about half mean $P_{VA}$.

$\dot{Q}_{DA}$ was pulsatile, but at normoxic values of $f_H$ flow was maintained throughout diastole (Fig. 2). Pulsatile dorsal aortic flow was monitored in three animals. Flow characteristics were similar in all three but a successful calibration was obtained only in one. Dorsal aortic peak pressure and flow seemed to be more nearly in phase compared with the situation in the ventral aorta (Fig. 2). The ratio of pressure and flow pulsatilities in the dorsal aorta was similar to the ratio in the ventral aorta (Table 1). The appearance of the pulse in the dorsal aorta lagged behind that in the ventral aorta by some 30–40 ms (Fig. 3). Interestingly, two of the five fish we used had a massive parasitic infection of the dorsal aorta, which made pressure recording extremely difficult (see Brill *et al.* 1987, for a complete discussion of this phenomenon).

$R_{TOT}$ was between 0.13 and 0.24 kPa ml$^{-1}$ kg$^{-1}$ min$^{-1}$ (mean 0.17±0.04 kPa ml$^{-1}$ kg$^{-1}$ min$^{-1}$) of which $R_G$ accounted for about 25 % in one fish and over 50 % in the others (Table 1). On average, $R_G$ was 48±15 % of $R_{TOT}$ ($N$=4). The impedance modulus for the ventral aorta displayed a sharp initial fall and then declined gradually over the next four harmonics (Fig. 4). Impedance phase was negative (pressure lagging behind flow oscillations), ranging between −0.8 and −1.1 rad at all pulsatile harmonics except for the first (Fig. 4). These relationships were similar for both fast (2.08 Hz) and slow (0.96 Hz) heartbeats. The analysis was limited to five harmonics because, for pressure, the fifth harmonic was only 1–2 % of the mean value and was close to the resolving power of the digitizer. In contrast, the fifth harmonic of flow was typically 5–10 % of the value at zero frequency. Hence, reconstitution of the original traces by summing the first five harmonics gave exceptional agreement for pressure but not for flow.

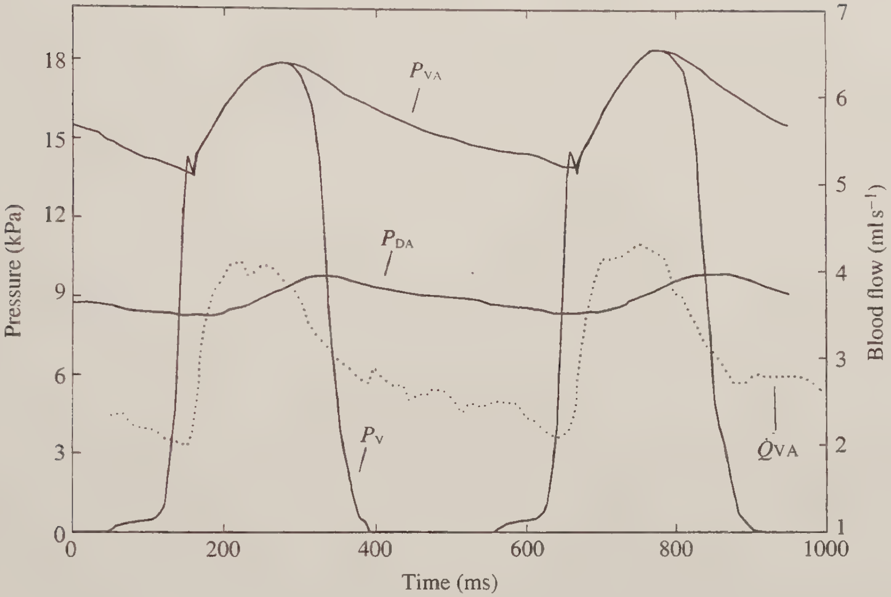

Fig. 3. Superimposed traces of ventral aortic pressure ($P_{VA}$), dorsal aortic pressure ($P_{DA}$), ventral aortic flow ($\dot{Q}_{VA}$) and ventricular pressure ($P_V$) in yellowfin tuna. Note that $P_V$ and $P_{VA}$ diverge at, or soon after, peak systole.

Table 2. *Heart rate and blood pressure of swimming yellowfin tuna*

| | Ventral aorta | | | Dorsal aorta | | |
|---|---|---|---|---|---|---|
| Heart rate (beats min$^{-1}$) | Systole (kPa) | Diastole (kPa) | Mean (kPa) | Systole (kPa) | Diastole (kPa) | Mean (kPa) |
| 130 | 14.3 | 9.5 | 11.1 | – | – | 6.8 |
| 102 | 12.4 | 10.4 | 11.1 | 6.8 | 4.9 | 5.6 |
| 108 | 13.1 | 11.3 | 11.9 | 6.5 | 5.2 | 5.6 |
| 102 | 15.1 | 10 | 11.7 | – | – | 8.4 |
| 102 | 15.2 | 10.5 | 12.1 | – | – | 7.6 |
| (108.8±12.1) | (14.0±1.2) | (10.3±0.7) | (11.6±0.5) | (6.7) | (5.1) | (6.8±1.2) |

Mean values ± S.E. are given in parentheses.

*Swimming fish*

$P_{VA}$ and $P_{DA}$ were recorded in five yellowfin tuna swimming laps of the doughnut-shaped tank. Lap times were not recorded. Heart rate averaged 108.8±12.1 beats min$^{-1}$. Mean ventral aortic pressure was 11.6±0.5 kPa and mean dorsal aortic pressure was 6.8±1.2 kPa (Fig. 5A; Table 2). Hence, mean $R_G$ in these swimming fish was 42 % of $R_{TOT}$. $\dot{Q}_{VA}$ was measured in three kawakawa. Zero flow was established by stopping water flow over the gills while the fish was being mechanically ventilated in the doughnut-shaped tank during recovery from anaesthesia. The flow profile recorded from a swimming kawakawa is shown in Fig. 5B. $\dot{Q}b$ averaged 67±40 ml min$^{-1}$ kg$^{-1}$ ($N$=3) at

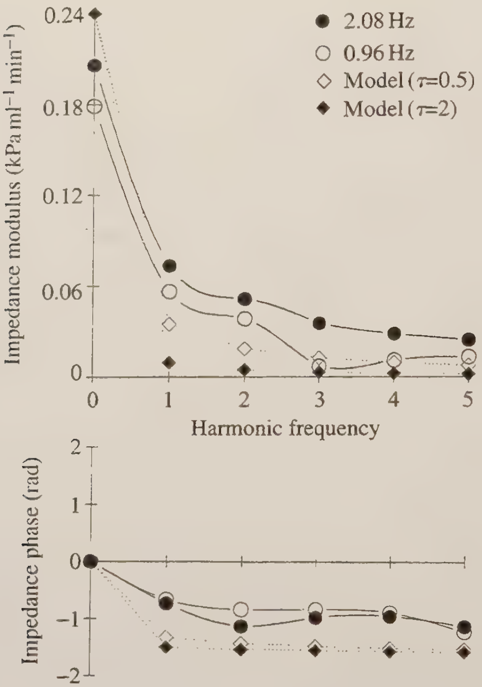

Fig. 4. Input impedance modulus and phase of the ventral aortic circulation of yellowfin tuna at normal (2.08 Hz, ●) and slow (0.96 Hz, ○) heart rates. The output of a Windkessel model at two different time constants ($\tau$) is shown for comparison. See text for further details.

a mean $f_{\mathrm{H}}$ of 128±48 beats min$^{-1}$. Hence, $Q_{\mathrm{S}}$ (0.54±0.2 ml kg$^{-1}$) was within the range of values recorded from anaesthetised yellowfin (Table 1). The kawakawa swam at a mean speed of 0.6 m s$^{-1}$, which was equivalent to 1.3 body lengths s$^{-1}$. An interesting feature of these recordings was that there was a bradycardia whenever this fish turned around to change its direction of swimming (Fig. 5B).

### *Analysis of a model circulation*

Experimentally determined impedance modulus ($Z$) and impedance phase ($\phi$) can be compared with impedance values obtained for a second-order $RC$ network (Satchell, 1971):

$$|Z|=\sqrt{\frac{(R_{\mathrm{G}}+R_{\mathrm{S}})^2+\omega^2(C_{\mathrm{DA}}\times R_{\mathrm{S}}\times R_{\mathrm{G}})^2}{(1-\omega^2R_{\mathrm{S}}\times R_{\mathrm{G}}\times C_{\mathrm{DA}}\times C_{\mathrm{VA}})^2+\omega^2[(R_{\mathrm{G}}\times C_{\mathrm{VA}})+(R_{\mathrm{S}}\times C_{\mathrm{DA}})+(C_{\mathrm{VA}}\times R_{\mathrm{S}})]^2}}\,, \tag{1}$$

where $C_{\mathrm{VA}}$ is ventral aortic compliance, $C_{\mathrm{DA}}$ is dorsal aortic compliance and $\omega=2\pi f$, where $f$ is harmonic frequency.

$$\phi=\tan^{-1}\left(\frac{\omega\times R_{\mathrm{S}}\times C_{\mathrm{DA}}\times R_{\mathrm{G}}}{R_{\mathrm{G}}+R_{\mathrm{S}}}\right)-\pi+\tan^{-1}\left(\frac{\omega[(R_{\mathrm{G}}\times C_{\mathrm{VA}})+(R_{\mathrm{S}}\times C_{\mathrm{DA}})+(R_{\mathrm{S}}\times C_{\mathrm{VA}})]}{-1+\omega^2C_{\mathrm{DA}}\times R_{\mathrm{S}}\times C_{\mathrm{VA}}\times R_{\mathrm{G}}}\right), \tag{2}$$

impedance phase is expressed for the case when $\omega^2C_{\mathrm{DA}}\times R_{\mathrm{S}}\times C_{\mathrm{VA}}\times R_{\mathrm{G}}>1$.

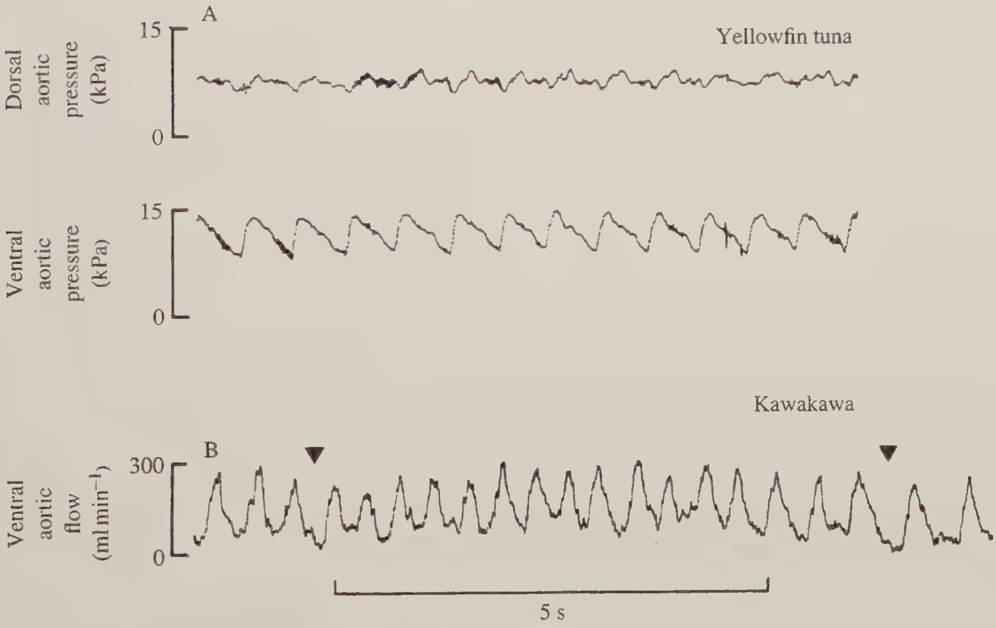

Fig. 5. (A) Dorsal and ventral aortic pressures in swimming yellowfin tuna. (B) Ventral aortic flow in a kawakawa. Note that flow fell to zero when the animal changed swimming direction (arrowheads). The time bar of 5 s applies to both A and B.

In the one tuna in which determinations were made, the ratio between pressure and flow pulsatilities was similar in the ventral and dorsal aortae, and $R_{\mathrm{G}}=R_{\mathrm{S}}$, so it is a reasonable assumption that compliance of the ventral ($C_{\mathrm{VA}}$) and dorsal ($C_{\mathrm{DA}}$) aortic systems were similar. Therefore, the time constant for the ventral aortic/gill circulation and dorsal aortic/systemic circulation will be the same. Unfortunately, previous model analyses have shown that the diastolic declines in pressure in both the ventral and dorsal circulations (the time constants, $\tau$) are not independent of one another (Jones *et al.* 1974; Langille *et al.* 1983). However, the time constant ($\tau$) for the dorsal circulation can be calculated by rearranging equation 8 of Langille *et al.* (1983):

$$(2\tau)^2=\left(\frac{PP_{\mathrm{VA}}}{PP_{\mathrm{DA}}}\right)^2-\left(1+\frac{R_{\mathrm{S}}}{R_{\mathrm{G}}}\right)^2, \tag{3}$$

where $PP$ is the difference between systolic and diastolic pressure in the ventral and dorsal aortae and

$$\left(1+\frac{R_{\mathrm{S}}}{R_{\mathrm{G}}}\right)^2<\left(1+\frac{PP_{\mathrm{VA}}}{PP_{\mathrm{DA}}}\right)^2.$$

Hence, if: $C_{\mathrm{VA}}\times R_{\mathrm{G}}=C_{\mathrm{DA}}\times R_{\mathrm{S}}=\tau$, then equation 1 reduces to:

$$|Z|=\sqrt{\frac{(R_{\mathrm{G}}^2)[4+(\omega\tau)^2]}{[I-(\omega\tau)^2]^2+9(\omega\tau)^2}}, \tag{1'}$$

and equation 2 to:

$$\phi = \tan^{-1}\left(\frac{\omega\tau}{2}\right) - \pi + \tan^{-1}\left(\frac{3\omega\tau}{-1+(\omega\tau)^2}\right). \qquad (2')$$

Curves describing impedance modulus and phase, obtained from the model analysis, are shown on Fig. 4 for two values of $\tau$ (0.5 and 2). For some of the anaesthetised tuna, $\tau$ averaged 2.06 ($N$=3). The curves show reasonably good agreement with those obtained from harmonic analyses of ventral aortic pressure and flow in anaesthetised yellowfin (Fig. 4).

## Discussion

The present data suggest that a simple, four-element 'lumped-parameter' model yields a reasonable estimate of pressure–flow relationships in the ventral aortic circulation of tuna as measured by arterial impedance. Although predicted values underestimate and overestimate measured values for impedance modulus and phase, respectively, the curves for both predicted and measured modulus and phase are of the same shape (Fig. 4). Unfortunately, our analysis of vascular impedance was limited by being taken to only five harmonics but, even at heart rates in excess of 2 Hz, there were no signs of the oscillations in modulus and phase which are so apparent in analyses of mammalian circulations. Pulse wave velocities will be slow, but will accelerate towards the gills because of the increased stiffness of the distal ventral aorta. Nevertheless, it is unlikely that pulse transmission will occupy a considerable portion of the cardiac cycle in fish of the size range used in these observations. Reflections make major contributions to wave transmission effects in mammals (O'Rourke, 1967; McDonald, 1974; Milnor, 1979; Jones, 1991) and are more pronounced for higher terminal resistances (van den Bos *et al.* 1982). The terminal resistance for the ventral aorta is the gill resistance which, in tuna, is similar to or less than the systemic resistance. Hence, tuna are like other fish in that a Windkessel dominates central haemodynamics despite heart rates that fall in the mammalian range. However, several factors contribute to the lack of wave transmission effects in our animals and it is entirely possible that some circumstances (i.e. large body mass, extremely high heart rate, low pulse wave velocity and high gill resistance) may promote considerable deviation from the Windkessel model.

Both pressure and flow in the dorsal aorta were pulsatile, although damped compared with ventral aortic waves. Pulsatile pressures and flows, with a loss of high-frequency components, have been recorded previously in the dorsal aorta of the cod (Jones *et al.* 1974). The ratio of pressure to flow pulsatilities in the one fish in which dorsal aortic flow was calibrated was similar in both ventral and dorsal aortic circulations, indicating similar compliance. The elasticity of the dorsal aorta is similar to that of the ventral aorta (D. R. Jones, R. W. Brill and C. L. Watson, unpublished observations) but the length of the dorsal circulation is much greater, thus illustrating the effectiveness of the contribution of the bulbus arteriosus to ventral aortic compliance.

Blood pressures in ventral and dorsal aortae in anaesthetised fish were similar to those in swimming fish. Pressures measured by us were close to those obtained by others (Lai *et al.* 1987; White *et al.* 1988; Bushnell and Brill, 1992). Mass-specific cardiac output (75 ml min$^{-1}$ kg$^{-1}$) was substantially lower than $\dot{Q}$b measured in spinalized yellowfin

(115 ml $\mathrm{min}^{-1}\,\mathrm{kg}^{-1}$) and skipjack tuna (132 ml $\mathrm{min}^{-1}\,\mathrm{kg}^{-1}$) (Bushnell and Brill, 1992), but was 2–3 times greater than that recorded by Lai *et al.* (1987), who used considerably bigger fish. Lai *et al.* (1987) suggest that a scaling factor for cardiac output of (body mass, kg)$^{0.81}$ might apply to albacore tuna which would give a $Q\mathrm{s}$ of 0.5 ml in a 1 kg albacore. This seems to be at the lower end of the range for tuna of this size, although all other determinations of $\dot{Q}\mathrm{b}$ in tuna have been made at a somewhat higher temperature which might, in itself, elevate $\dot{Q}\mathrm{b}$. At heart rates in excess of 90 beats $\mathrm{min}^{-1}$, flow in the ventral aorta was continuous. This made determination of zero flow difficult except when heart rate slowed in the absence of large changes in ventral aortic blood pressure. Lai *et al.* (1987) make no mention of how they established zero flow in their fish, and it is possible that they underestimated the continuous flow component.

Tuna have exceptionally large hearts which beat at a higher frequency and generate greater pressures than those of most teleosts (Kanwisher *et al.* 1974; Poupa *et al.* 1981; Breisch *et al.* 1983; Lai *et al.* 1987). Maximum heart rates reported for swimming tuna are around 260 beats $\mathrm{min}^{-1}$ (Kanwisher *et al.* 1974). In comparison, heart rates in kawakawa, swimming at low speed, averaged 128 beats $\mathrm{min}^{-1}$, somewhat higher than the range of 40–85 beats $\mathrm{min}^{-1}$ reported for slowly swimming yellowfin and skipjack tuna (Bushnell and Brill, 1991). However, heart rates in excess of 250 beats $\mathrm{min}^{-1}$ have been observed in paralyzed, artificially ventilated tuna (Brill, 1987) and heart rates obtained from our swimming kawakawa were similar to those obtained from anaesthetized or spinalized tuna (Breisch *et al.* 1983; Bushnell *et al.* 1990). Obviously, heart rate does not appear to correlate well with the fish's level of activity.

In fishes, unlike many higher vertebrates, the ventricle is filled by atrial contraction and the atrium, in turn, is filled by the sinus venosus or by the kinetic and potential energy of the flowing venous blood (Farrell and Jones, 1992). Atrial contraction lasts about 70–100 ms whereas the systolic ejection phase takes 250–300 ms (Table 1). Hence, if there is no diastolic period (i.e. the sinus venosus fills, and then fills the atrium during ventricular ejection), the theoretical maximum heart rate in tuna will be approximately 250–300 beats $\mathrm{min}^{-1}$, which agrees with maximum recorded heart rates (Kanwisher *et al.* 1974; Brill, 1987).

At these high heart rates there could be a problem of filling and emptying the ventricle. Lai *et al.* (1987) reported that tuna have large negative intrapericardial pressures, which assist in cardiac filling. We feel, however, that the existence of large negative intrapericardial pressures are unlikely in an animal that exercises continuously. Tuna should not need much help with venous return other than that provided by muscular activity. Given that the heart can fill, there is still a problem with ejecting a large stroke volume. Stroke volume can be increased by phenylephrine injection. In the present experiments, $Q\mathrm{s}$ increased by 30 % but the systolic ejection phase increased by 50 % compared with that before inotropic stimulation. Obviously, there seems to be an antagonistic rather than synergistic interplay between increasing inotropic and chronotropic forces in tuna.

The heart is pyramidal with a compact myocardium surrounding an inner trabeculate (spongy) myocardium (Sanchez-Quintana and Hurle, 1987). The muscle fibres in the compact layer are arranged in longitudinal and circular bundles (Sanchez-Quintana and

Hurle, 1987). On the ventral faces of the ventricle, the superficial fibres are arranged longitudinally but on the caudal face they are predominantly transverse. An inner layer of fibres is arranged circularly around the ventricles. Hence, during systole there is probably a reduction in both longitudinal and transverse diameters of the ventricle. Further, many fibres are inserted into a bulbo-ventricular fibrous ring and could actively open the bulbo-ventricular orifice (Sanchez-Quintana and Hurle, 1987). The observation that ventricular and ventral aortic pressures begin to diverge soon after peak ventricular systole indicates that active tension on the bulbo-ventricular valve may be released at this time.

The contribution of compact and spongy myocardium to the generation of high systolic pressures is equivocal. Johansen (1965) envisaged the trabeculate hearts of ectotherms as a group of pumps in parallel with one another. It has been suggested that Laplacian relationships might not govern trabeculate hearts in the same way that they govern endotherm hearts, in which the ventricles are hollow and have compact walls (Seymour, 1987). However, each individual lacuna in the trabeculate portion of the heart will be governed by Laplacian relationships. Furthermore, because the radius of each lacuna is small, pressure will be generated at a considerable mechanical advantage compared with hearts consisting of solely compact myocardium. The rate of pressure generation seems to be very fast in compact/spongy hearts, although the values we obtained are probably too high by 50–100 % because of the low-frequency response of our recordings (McDonald, 1974). This artefact is confirmed by the presence of ‘spikes’ and after-vibrations on some of our pressure records. Nevertheless, a $dP/dt$ of half our measured rate would still compare favourably with $dP/dt$ in most mammals. There must be costs associated with trabeculate hearts because not all animals use this design. The ability to increase stroke volume by reducing end-diastolic volume is a major factor contributing to increased cardiac output in mammals, and this may be seriously restricted in trabeculate hearts.

The above limitation on our estimation of $dP/dt$ notwithstanding, our recordings are of sufficiently high fidelity to be compared critically with those of others. For instance, ventricular diastolic pressures were usually zero, except after atrial contraction, when pressures rose to between 0.15 and 0.76 kPa. However, others have reported ventricular diastolic pressures ranging from −0.5 to +6.2 kPa (Breisch *et al.* 1983; Lai *et al.* 1987; White *et al.* 1988). Negative ventricular pressure could result from a negative intra-pericardial pressure (Lai *et al.* 1987), but negative venticular pressures were not seen in our fish. Surprisingly, two studies have reported that dorsal aortic diastolic pressures can be above those in the bulbus (Breisch *et al.* 1983; White *et al.* 1988). This would reverse the pressure gradient for flow through the gills. However, neither our pressure nor our flow recordings suggested such a situation. Finally, $R_G$ in both anaesthetised and swimming fish was usually between 40 % and 50 % of $R_{TOT}$, which was not as high as $R_G$ values calculated for spinalized skipjack (60 %) and yellowfin (68 %) tuna (Bushnell and Brill, 1992), but was much higher than the mean value of 26 % recorded by Lai *et al.* (1987) or the 6 % that can be estimated from the data of White *et al.* (1988). Nevertheless, the massive increase in surface area of the gills in tuna is achieved without much cardiovascular cost for the resistance presented to blood flow by tuna gills is similar to that of trout gills (Kiceniuk and Jones, 1977).

Although massive parasitic infections of the dorsal aorta made pressure recording difficult, they did not seem to be having any deleterious effect on the tuna. Brill *et al.* (1987) suggested that these infections cause a large increase in resistance in the dorsal aorta, although this conclusion was confounded by the significant resistance of the tubing in their perfusion apparatus and also by the extreme pressure required to open the parasitized vessel for flow. However, on a plot of flow *versus* pressure, resistance is given by the slope of the line. The data of Brill *et al.* (1987) indicate that resistance of the parasitized segment was no more than three times that of the unparasitized vessel. Because the flow resistance in a large vessel is small, it can be concluded that the parasites have a negligible effect on either pressure or flow.

Maximum $\dot{V}_{O_2}$ in tuna is close to $30\,\mathrm{ml\,min^{-1}\,kg^{-1}}$ (Gooding *et al.* 1981), some 10 times the 'resting' rate, yet maximum $\dot{Q}$b appears to be only two or three times that in anaesthetised fish, largely because of the antagonistic interference between *f*H and *Q*S. Hence, arteriovenous oxygen difference must increase markedly during exercise. Tuna differ from most teleosts by having a high blood oxygen-carrying capacity (Jones *et al.* 1986). The potential to increase the arteriovenous oxygen difference must be used to good effect because, during swimming, $\dot{Q}$b was less than in anaesthetised preparations. In fact, the arteriovenous oxygen difference in anaesthetised or spinalized tuna is extremely low (Bushnell and Brill, 1991), indicating that $\dot{Q}$b in these fish should not be regarded as a 'resting' value.

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# OVERVIEW OF THE GROUNDFISH FISHERIES OF THE WEST COAST OF THE UNITED STATES OF AMERICA

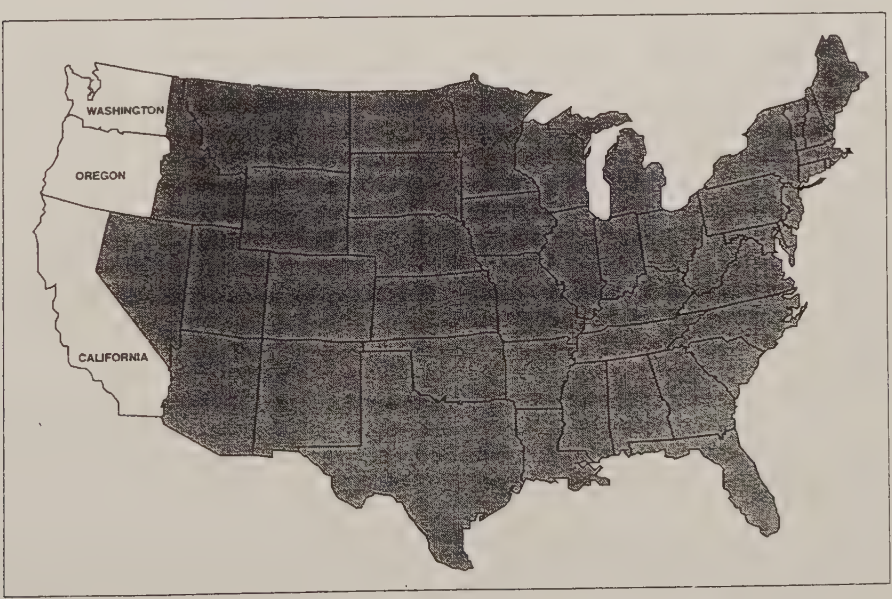
William H. Lenarz[*]

In this paper I present an overview of the groundfish (demersal) fisheries of the West coast of the United States of America. This area includes the waters within 200 miles of the coasts of the states of Washington, Oregon and California, Figure 1. While the continental shelf is narrow, the area is productive because of the California Current and upwelling that occurs during spring and summer.

The fisheries are diverse. More than 50 species of groundfish are captured by hundreds of commercial vessels. Vessel types include gillnetters, hook and line vessels, small bottom trawlers and large trawlers that use both bottom and midwater trawls. In addition there are more than 2 million recreational fishermen and, while not all of these fishermen fish for groundfish, recreational landings of groundfish exceed 15 million fish.

The fisheries have also changed considerably over the years. Domestic landings ranged from less than 50,000 mt in 1973 to almost 300,000 mt in 1991, Figure 2. Many stocks were lightly exploited in 1973. A combination of improved markets, expansion of the economic zone to 200 miles in 1977, and improved fishing techniques resulted in rapid increases in landings. By 1982 it was obvious that many stocks should not be fished down to lower levels. It was necessary to place annual landing limits on several important stocks in 1983. Since I am involved in making management

FIGURE 1 **Map of United States of America, exclusive of Alaska and Hawaii, emphasizing the states of California, Oregon and Washington.**



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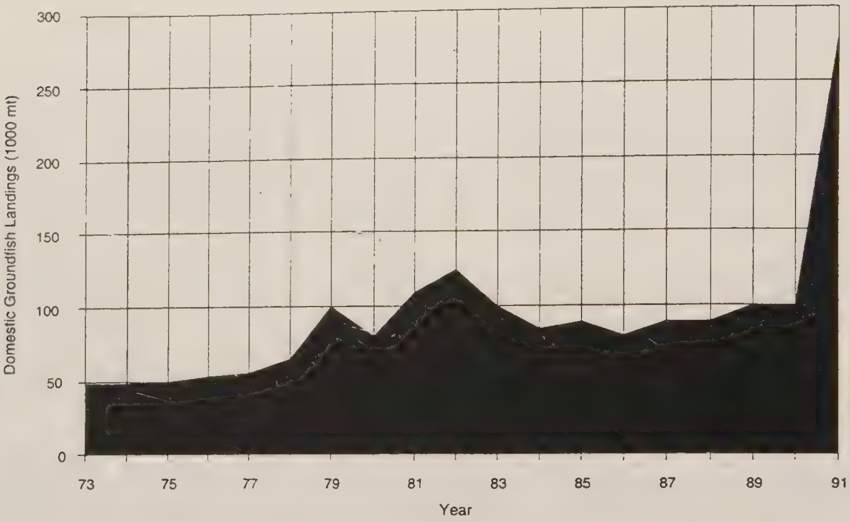
[*] *Southwest Management Council, Kentfield, E.U.A*

FIGURE 2 **Domestic landings of groundfish off the west coast of the U.S., 1973-1991.**



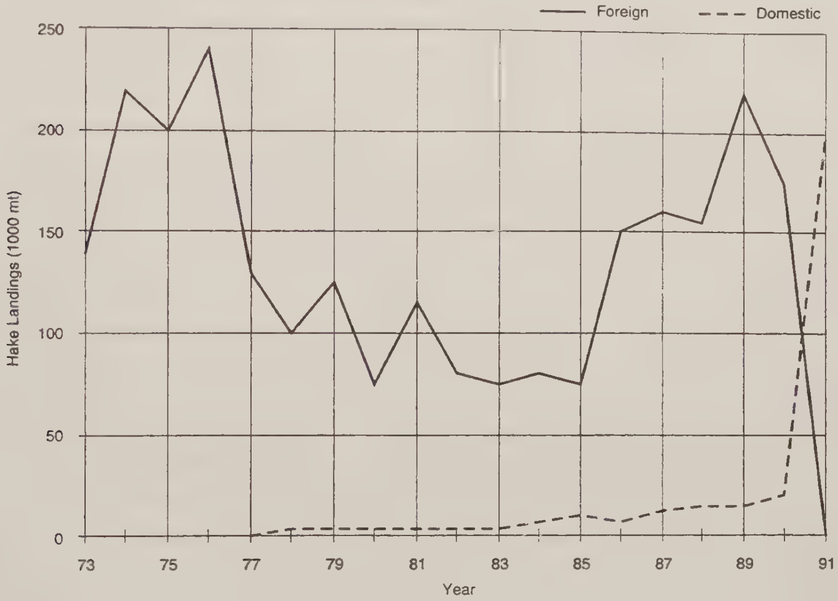
recommendations, I would like to be able to say that the large increase in 1991 landings is directly the result of our excellent management decisions.

In actuality several factors were involved in the increase. Combined foreign and domestic landings did not show the rapid increase. The increase in domestic landings was at the cost of a similar decrease in landings delivered to foreign processors of a very important species, Pacific hake (Family Merlucciidae; *Merluccius productus*). Until 1991 most Pacific hake were processed by foreign vessels and sometimes captured by foreign fishermen, figure 3. There has been a national policy to convert both the catching and processing of all fish from U.S. waters to domestic concerns. However until recently there was little domestic interest in processing Pacific hake, because a parasite causes difficulties in producing a high quality product. These problems were solved and large domestic factory trawlers and processor vessels began moving into the area from Alaskan waters in late 1990 and the fishery became completely domestic in 1991. The land based processing industry is also increasing rapidly. Our management people now have the difficult task of allocating the catch between factory trawlers, smaller trawlers delivering catches to processing vessels, and other trawlers delivering catches to land based processors.

The large increase in domestic landings of hake is also partly the result of good management policies and reliable stock assessments. Since 1977, catch restrictions have been based on assessments using data from hydro-acoustic surveys and catch samples. A healthy stock was maintained and was available when it became economically feasible for domestic processors to utilize hake.

The fisheries for other types of groundfish have also changed, Figure 4. Landings of the rockfish group (Family Scorpaenidae) show the greatest changes since 1973. Sixty species of rockfish (*Sebastes* spp.) and two species of thornyheads (*Sebastolobus* spp.) occur off our coast. These species range from the robust, sedentary and usually solitary gopher rockfish (*S. carnatus*) to the streamlined, semi-pelagic and very

FIGURE 3 **Domestic and foreign landings of Pacific hake off the west coast of the U.S., 1973-1991.**



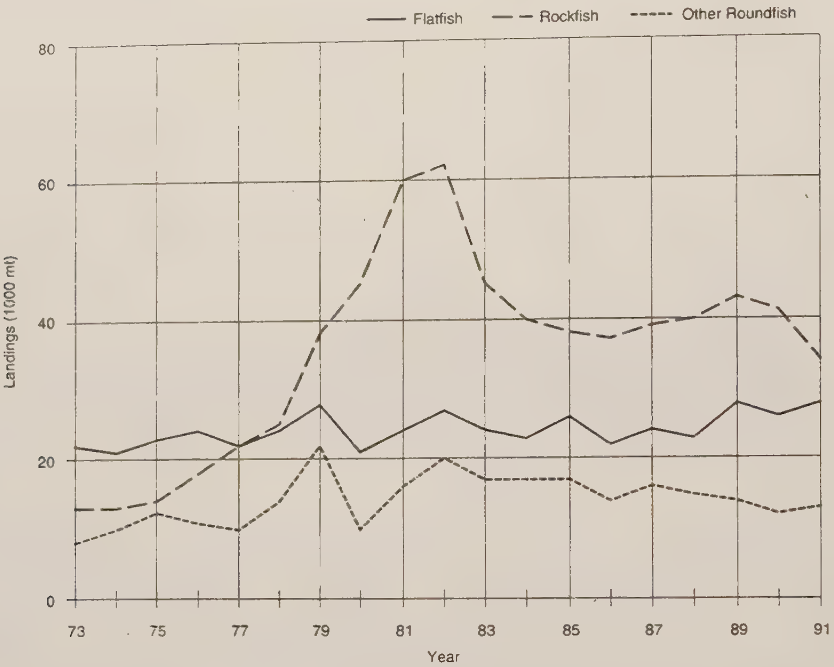
abundant shortbelly rockfish (*S. jordani*). While numerous rockfish species occur off our coast the landings are dominated by eight species.

The rapid increase in landings of rockfish through 1982 is the result of increased markets and improved fishing techniques. Landings of widow rockfish (*S. entomelas*) had the greatest change. They increased from about 1000 mt in 1978 to about 26,000 mt in 1982, and were reduced to 10,000 mt in 1983 when it became necessary to protect the stock from depletion. The increase in landings between 1986 and 1989 was the result of an improved market for thornyheads. It also proved necessary to restrict landings of thornyheads in order to protect the stocks.

The landings of other roundfish have also varied considerably. Much of the variation between 1973 and 1982 is due to changing market conditions for sablefish (Family Anoplopomatidae; *Anoplopoma fimbria*). Sablefish is another species that needs protection from overfishing and landings have been constrained by regulations since 1983. Sablefish are very valuable and division of the catch between trawl, and nontrawl gears (longline and traps) has been a difficult management issue. Very recently there has been increased interest in Pacific grenadier (Family Macrouridae; *Coryphaenoides acrolepis*) and I expect that they will become more important in the landings.

The landings of flatfish are not as dynamic as the other groups. The increased landings in recent years are mostly the result of an improved market for arrowtooth flounder (Family Pleuronectidae; *Atheresthes stomias*). However, more than 50% of the flatfish landings are comprised of Dover sole (Family Pleuronectidae; *Microstomus pacificus*) and most of the earlier fluctuations are due to changing market conditions for this species.

FIGURE 4 **Landings of flatfish, rockfish and other roundfish off the west coast of the U.S., 1973-1991.**



Research on groundfish is as diverse and has changed as much as the fisheries. The amount of research increased considerably as the fishery expanded. Prior to 1977 biological composition sampling of landings of many species was minimal and sporadic. We now have a satisfactory sampling program for most of the important species. Economists monitor the industry with a combination of required reporting and special studies. Coastwide trawl surveys have been conducted on a tri-annual basis for upper slope and shelf species since 1977. A hydro-acoustic survey for Pacific hake also is conducted on a tri-annual basis. Trawl surveys have been conducted along most of the coast for deepwater species such as Dover sole and sablefish. Submersibles and remotely operated vehicles have been used to calibrate the deep water trawl surveys. Coastwide trap surveys are conducted for sablefish.

It has proven very difficult to estimate the abundance of rockfish from standard trawl or hydro-acoustic surveys because their behavior. We are conducting an annual young-of-the-year midwater trawl survey off California to estimate recruitment strength of important rockfish species. We are attempting to use larval surveys to extend the egg production method of estimating spawning biomass to live bearers such as rockfish. Oceanographic sampling is a part of these studies and oceanographers are working closely with us to relate fish distributions and reproductive success to oceanographic features. We are also closely following the efforts of researchers in Alaska to develop hydro-acoustic and other methods to estimate rockfish abundance. Fieldwork for a large study on mesh size that included many trips on commercial fishing vessels was recently completed to provide data to evaluate proposed changes in mesh size regulations.

Results of the field work are utilized by scientists at several laboratories to estimate the condition of stocks and make recommendations for managing the fishery. The stock synthesis model is used for catch at age analyses that form the basis for most of our assessments. Economists estimate the impact of proposed regulations with a variety of formal and informal analyses. We also develop computer simulation models to evaluate and further develop assessment and management techniques.

The Pacific Fishery Management Council considers recommendations from the scientists, fishing industry, legal advisors, enforcement agencies, and general public to formulate its management recommendations. The Council's recommendations are then subject to approval by the U.S. Department of Commerce. Usually recommendations by the scientists are followed by the Council and recommendations by the Council are approved by the Department of Commerce. The management regulations are then implemented by federal and state enforcement agencies.

Since many of our species are long lived, 50 to 100 years, the stocks can not support heavy fishing rates. It has not been an easy task to maintain both a healthy fishing industry and healthy stocks of fish. Beside gear restrictions and annual quotas it has been necessary to impose restrictions on the size and frequency of individual landings in order to insure the long open fishing seasons that our fresh fish markets desire. The landing limits cause discards of fish from catches that are unintentionally above the landing limits. As the fishing power of the fleet has increased, it has become very difficult to balance the risk of increased discards caused by restrictive landing limits against the early closure of fishing seasons that result when landing limits are not sufficiently restrictive.

Many people in the fishing industry and management believe that the number of vessels participating in the fishery should be restricted to present levels or reduced. While most of the fish stocks are healthy, almost all are already fully fished, and there is much more fishing power than is needed to take the allowable catch. The Council is in the final stages of preparing a recommended program to prevent the entry of new vessels in to most components of the fishery and hopes to implement the system by 1994. The Council has also begun to develop proposals for an Individual Transferable Quota system.

It has been fascinating to observe the changes in the fishery and particularly to witness limited access to the groundfish fishery change from being a subject that wasn't discussed in polite company to being a popular option for management of the fishery. While this management option is still controversial within the fishing industry, it has many supporters including some of the largest fishermen organizations. I think that events in this fishery during the next decade also will also be very interesting to follow.

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# A DAILY FECUNDITY REDUCTION METHOD OF BIOMASS ESTIMATION WITH APPLICATION TO DOVER SOLE *MICROSTOMUS PACIFICUS*

*N. C.-H. Lo, J. R. Hunter, H. G. Moser and P. E. Smith*

## ABSTRACT

A daily fecundity reduction method was applied to *Microstomus pacificus,* commonly known as Dover sole, a pleuronectid flatfish of the upper continental slope (200 to 1,500 m) of the west coast of North America. This method was developed for estimating adult biomass of fishes with determinate annual fecundity and utilizes the daily decline in reproductive potential of the population and the numbers of planktonic eggs. Daily decline in reproductive potential was estimated from the decline of the product of the standing stock of advanced oocytes and the numbers of females with reproductively active ovaries. Daily production of planktonic eggs was estimated from the numbers of eggs in quantitative oblique plankton tows. We describe the survey design, data assembly, statistical estimation procedures, and the possible biases due to the limitation of surveys.

Our objective is to apply a new daily egg production method designed for fishes of determinate annual fecundity (Lo et al., 1992) to Dover sole, *Microstomus pacificus,* a commercial flatfish occurring along the upper continental slope of North America. The potential annual fecundity of Dover sole is determinate (Hunter et al., 1992), consequently, the daily decline in the number of yolked oocytes in the ovary (E) can be considered to be equivalent to the daily rate of spawning. This concept is the heart of the new daily egg production method described by Lo et al. (1992). The new method is called the daily fecundity reduction method (DFRM) to distinguish it from other daily egg production methods in which spawning rates are measured directly using estimates of batch fecundity and spawning frequency. A synopsis of the general concept was presented by Lo et al. (1992). We present the details of procedures for applying the DFRM to Dover sole including survey designs and computations of estimates of biological parameters and their variances.

The major difference between the daily fecundity reduction method and the other daily egg production methods is how daily spawning rates are estimated. Application of the daily egg production method to Dover sole required several modifications since the method was designed originally for northern anchovy (*Engraulis mordax*) and other pelagic multiple spawners. Dover sole spawn at bottom depths of 600 to 1,500 m and their eggs are distributed throughout the water column. Thus, quantitative plankton tows, beginning near the sea bottom at depths as great as 1,500 m and ending at the surface, were required and the developmental rate of eggs had to be adjusted for the temperatures encountered by the eggs during their ascent. Dover sole eggs incubate at much lower temperatures (5 to 13°C) and the egg state lasts longer (20 to 30 d) than northern anchovy (2 to 3 d; Lo, 1985). Thus, transport of Dover sole eggs by currents in and out of the study area was a much more likely source of bias for Dover sole than for anchovy.

In the application of the daily egg production method to northern anchovy and Pacific sardine (*Sardinops sagax*), random mixing of fish of all sizes and reproductive states was assumed. This assumption could not be made for Dover sole because the size, age, and reproductive activity of Dover sole were known to increase with depth (Hunter et al., 1990). Thus, bathymetry was considered in the design of the sampling plan and computations. Dover sole are neither as abundant nor as fecund as northern anchovy. The northern anchovy stock (ca. 0.5 to 1.0 × $10^6$ mt) produces about 5,000 to 10,000 eggs per gram of female per year, while the Dover sole in our study area (about 17,000 mt according to Butler et al., 1989) produces only 50 to 100 eggs per gram female weight per year, even though they spawn about 10 times. Thus, the 25 cm diameter plankton net used for anchovy egg production surveys, was not suitable because it would not filter a sufficient volume of water and a larger net was required.

## MATERIALS AND METHODS

*Model.*—The model for the daily fecundity reduction method is:

$$B = (P_0 \cdot A)/[(R/W) \cdot D_t \cdot 10^6] = P_0 \cdot A/K \tag{1}$$

with an approximate coefficient of variation (CV) for the estimate of biomass as:

$$CV(B) \approx \{CV(P_0)^2 + CV(K)^2 - [2 \cdot COV(P_0 \cdot K)/(P_0 \cdot K)]\}^{0.5} \tag{1a}$$

where B is the biomass (mt) for area A, $P_0$ is the daily production of eggs per 10 $m^2$ sea surface area estimated from egg abundance adjusted for their development time and mortality during incubation, A is the size in 10 $m^2$ of the survey area, $K = (R/W) \cdot D_t \cdot 10^6$ in the denominator of (1) is daily population fecundity in units of eggs·$mt^{-1}$·$day^{-1}$, where R is the female fraction of the population by weight, W is the average female weight (g), $D_t$ is the daily fecundity per female at day of the year t and is expressed as

$$D_t = d(E \cdot G)/dt = E_t \cdot dG/dt + G_t \cdot dE/dt.$$

The constant $10^6$ converts grams to metric tons. E is the number of advanced yolked oocytes in the ovary (total fecundity), G is the fraction of females that have ovaries containing advanced yolked oocytes (fraction of females with active ovaries), and t is the elapsed time in days over which changes in G and E are monitored.

A key difference between this model and models for the annual egg production model (AEPM) (Saville, 1964) and daily egg production method (DEPM) (Lasker, 1985) is in the computation of adult reproductive rates. Our model differs from the AEPM model because total fecundity (E) is computed on a daily, rather than an annual, basis and differs from the DEPM model because the number of eggs spawned per day, or daily fecundity, is computed from the decline in total fecundity over the spawning season, rather than from the direct product of spawning frequency (S) and batch fecundity (F).

In the DFRM model (eqn 1), we use two variables (E and G) to measure the decline in total fecundity. As any female taken in a trawl can be included in the denominator of the fraction of females with active ovaries (G), it follows that the biomass (B) is an estimate of the total adult biomass vulnerable to our trawl, which includes all adult fish and an unknown fraction of the juveniles. In the daily egg production method used for anchovy, only the spawning biomass was estimated. While direct formulas were used to compute estimates of parameters and their variances, resampling methods such as the jackknife and bootstrap were also used to estimate the variance of biomass, covariances of adult parameter estimates, and the bias of estimates of parameters (Efron, 1982) because some covariance terms cannot be estimated from the direct method.

*Survey Design.*—The survey area extended from Point Conception to Monterey Bay, an area of 14,172 $km^2$ (Fig. 1). This area is a small fraction of the total Dover sole habitat, which extends from the Bering Sea to Baja California, Mexico (Eschmeyer et al., 1983). However, tagging studies indicate a very low level of coastal movement of adults (Quirollo and Kalvass, 1987). The survey area was sampled by trawl during five cruises between 1985 and 1988 (Table 1). A 400-mesh Eastern trawl was used on all cruises to collect Dover sole (Butler et al., 1989). A line transect sampling design was used in 1987 (Jan 8 to Feb 17) to investigate bathymetric patterns, and a random sampling design was used in 1988 (Feb 22 to April 10) as a pilot biomass estimation survey (Fig. 1). Prior to 1987, trawling for Dover sole was a secondary cruise objective, and trawls were taken opportunistically without a formal survey design.

During 1985 and 1986, up to 25 Dover sole from each trawl were randomly selected for sex determination. Additional ovaries were randomly selected so that 25 female Dover sole from each trawl were examined to determine the fraction of females with active ovaries. During 1987 and 1988 we measured, weighed, and classified the ovaries of a random sample consisting of up to 100 Dover

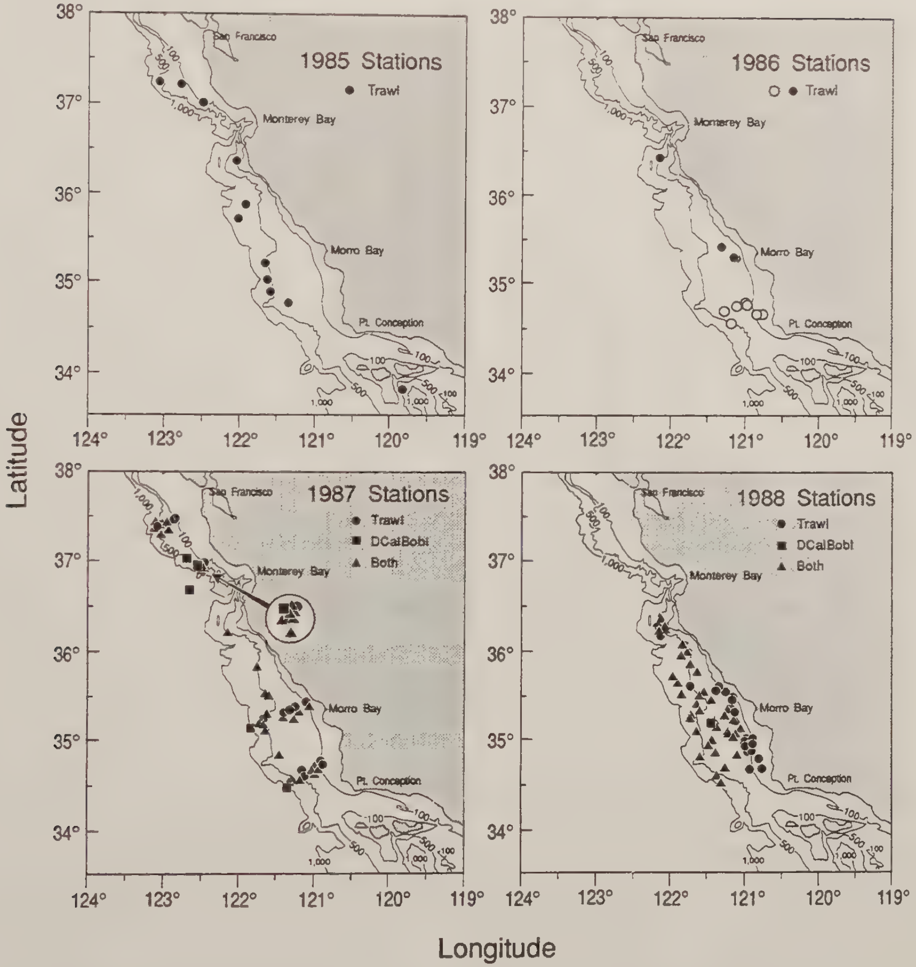
1985 Stations
● Trawl
1986 Stations
○ ● Trawl
1987 Stations
● Trawl
■ DCalBobl
▲ Both
1988 Stations
● Trawl
■ DCalBobl
▲ Both
San Francisco
Monterey Bay
Morro Bay
Pt. Conception
100
500
1,000
38°
37°
36°
35°
34°
124°
123°
122°
121°
120°
119°
Latitude
Longitude

Figure 1. Stations sampled for Dover sole eggs and adults in 1985 to 1988. For 1986, open circles are stations occupied in March–April, and solid circles are stations occupied in May–June.

sole. Sex ratios by weight were estimated, and the total weight of Dover sole in each trawl catch was recorded.

*Plankton Tows.*—At each station on the 1987 and 1988 cruises, we sampled Dover sole eggs using surface (MANTA) tows, standard oblique bongo (CalBOBL) tows to 210 m depth, and oblique deep bongo (DBOBL) tows, which sampled the entire water column. The DBOBL tow encompassed the vertical range of Dover sole eggs for the purpose of estimating egg production rates. Mature Dover sole spawn near the ocean floor at depths of 600 to 1,500 m, and after fertilization the eggs rise, some reaching the surface. Standard procedure was to take a CalBOBL and a DBOBL tow at every station having a bottom depth >200 m and a CalBOBL tow only at stations where bottom was <200 m deep. A total of 118 CalBOBL tows and 86 DBOBL tows was taken during the 1987 and 1988 cruises and two CalBOBL tows and one DBOBL tow were excluded from data analyses because of incomplete data (Table 1). We sorted the entire contents of most tows for Dover sole eggs. When plankton were unusually dense, ca. 50% of the contents of the CalBOBL and 25% of the DBOBL were sorted.

We used a standard haul factor (SHF) to convert catches of eggs by oblique CalBOBL or DBOBL tows to estimates of egg density (Appendix 1). The lower SHF for DBOBL tows reflects the greater

Table 1. Sources of data used to estimate each of the parameters used in egg production method for Dover sole from central California. Egg production parameters P through E are defined in the text (+, cruise providing data for estimating parameter; −, data not available)

| | | | Number of tows | | | | | | | Egg production parameters | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Plankton | | | | | | | | | | | | | |
| | | | Bongo | | Deep Bongo | | Trawl | | | | | | G | | | |
| Cruise Year | Month | Sampling type | Pos | Total | Pos | Total | Pos | Total | Depth (fm) | P | W | R | Deck | Lab | Hist | E |
| 85 | 12 | Opportunistic | 0 | 0 | 0 | 0 | 11 | 17 | 94–704 | 0 | + | + | − | + | + | + |
| 86 | 03–04 | Opportunistic | 0 | 0 | 0 | 0 | 8 | 10 | 52–500 | − | − | + | − | + | + | − |
| 86 | 05–06 | Opportunistic | 0 | 0 | 0 | 0 | 3 | 6 | 175–537 | − | + | + | − | + | + | − |
| 87 | 01–02 | Line Transect | 7 | 54 | 21 | 42 | 49 | 55 | 99–705 | + | + | + | + | + | + | + |
| 88 | 02–04 | Stratified Random | 16 | 62 | 22 | 44 | 51 | 63 | 38–602 | + | + | + | + | − | − | + |
| Total | | | 23 | 116 | 43 | 86 | 122 | 151 | | | | | | | | |

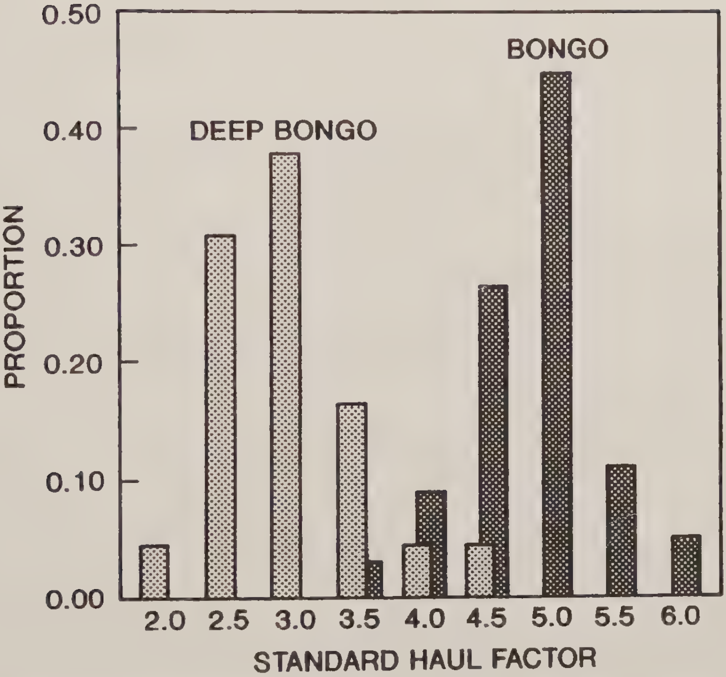

Figure 2. Relationship between standard haul factor (SHF) for the deep bongo and standard bongo net tows.

volume of water filtered per unit depth, not the greater depth (Fig. 2) and the faster speed (1.05 $m \cdot s^{-1}$ rather than 0.85 $m \cdot s^{-1}$ for the standard tow (CalBOBL)). The faster tow allows the ship speed to be controlled more precisely.

The reliability of this sampling procedure depends on the actual vertical distribution of eggs. If eggs were randomly distributed with depth, then the assumption of equal sampling at each depth interval would be unnecessary. If eggs were distributed non-randomly over broad depth zones (50+ m), episodes of over-sampling would probably compensate for episodes of under-sampling, resulting in little or negligible bias. On the other hand, if the egg layer were compact, imprecision could arise from sampling error.

*Plankton Sample Processing and Egg Staging.*—Each plankton sample was preserved in 5% buffered formalin immediately after each tow. Fish eggs and larvae were later removed from the plankton samples and preserved in 3% buffered formalin. Dover sole eggs were identified in samples by the following: 1) large size (ca. 2.0 to 2.6 mm shell diameter), 2) large perivitelline space, 3) smooth shell, 4) lack of oil globule, 5) homogeneous yolk, and 6) distinctive pigmentation on late stage embryos. Eggs were staged using a modification of the method developed for northern anchovy (Moser and Ahlstrom, 1985). Stages were defined by morphological criteria chosen from the sequence of changes that occur during embryogenesis (Table 2).

The stages of eggs were converted to ages according to a temperature-dependent egg development model (Appendix 1). Data from both CalBOBL and DBOBL were used to model the egg mortality curve. For the stations where both CalBOBL and DBOBL tows were taken, we computed number of eggs$\cdot$10 $m^{-2}$ (y) for each age group as (Fig. 3):

$$y = (y_1 + y_{2u})/2 + y_{2L}$$

where $y_1$ is the number of eggs per 10 $m^2$ of CalBOBL, $y_{2u}$ is the number of eggs per 10 $m^2$ of DBOBL allocated to <200 m level, and $y_{2L}$ is the number eggs per 10 $m^2$ of DBOBL allocated to >200 m level (Appendix 1). We fitted a Pareto decay function to the number of Dover sole eggs at age because the mortality of younger eggs was higher than that of older eggs. The mortality curve for Dover sole eggs was

Table 2. Criteria for assigning developmental stages to Dover sole eggs

| Stage | Criteria |
|---|---|
| I | fertilization to initial cell division |
| II | first cell division and blastodisc formation |
| III | blastomeres minute and blatodisc appears as tissue |
| IV | germ ring extends ⅓ around yolk |
| V | germ ring extends ⅔ around yolk |
| VI | blastopore closure |
| VII | tail tip rounded and begins to separate from yolk |
| VIII | tail length = ½ head length |
| IX | tail length = head length |
| X | tip of tail reaches ½ yolk diameter |
| XI | tip of tail reaches ¾ yolk diameter |
| XII | tip of tail reaches midline of forehead; to hatching |

$$P_t = P_0 \cdot (t + 1)^{-\beta} \tag{2}$$

and

$$z_t = \beta/(t + 1)$$

where $P_t$ = the number of eggs per 10 m² in the day t age group, $P_0$ = the number of newly spawned eggs per 10 m², $\beta$ = the mortality coefficient and the daily instantaneous mortality rate at age 0, and $z_t$ = daily instantaneous mortality rate at an age of t days. We used a nonlinear regression procedure of statistical software package BMDPAR (Dixon, 1988) to produce estimates of $P_0$ and $\beta$.

*Adult Parameters.*—FEMALE WEIGHT (W). Estimates of average fish weight were computed from random samples taken from trawls. The number of fish in a random sample was 25 in 1985 to 1986 and 100 in 1987 to 1988. Total length (mm) of Dover sole in these samples was always measured, but not all fish were weighed. For specimens that were not weighed, weight was computed from a length-weight relationship derived from 1,516 Dover sole taken in the 1987 and 1988 cruises (Appendix 1). Average female weight (W) was computed for each stratum as:

$$W = \sum (q_i \cdot x_i)/\Sigma q_i \tag{3}$$

where $q_i$ = number of females in the sample taken from the ith trawl, and $x_i$ = the average female weight in the sample.

FEMALE FRACTION OF POPULATION (R). The female fraction of the population by weight (R) was estimated by the weighted mean of the female fraction in individual trawls by equation 3 where, for the ith trawl, $q_i$ is the total weight of Dover sole sampled and $x_i$ is the female fraction, computed as total female weight in the sample divided by the total sample weight.

TOTAL FECUNDITY (E). Total fecundity (E) was estimated as the product of the ovary weight in grams and the number of advanced oocytes per gram of ovarian tissue. We used the gravimetric method to estimate the number of advanced oocytes per gram of ovarian tissue. Advanced oocytes were counted in each of two weighed tissue samples. Previous statistical analysis indicated that two ovarian tissue samples from each of 70 to 80 females were adequate because advanced yolked oocytes are randomly distributed within the ovary of Dover sole (Hunter et al., 1992).

Advanced yolked oocytes were counted and measured using a digitizer linked by a video camera system to a dissection microscope. Advanced yolked oocytes were distinguished from other yolked oocytes by their high yolk density when viewed on the television screen. Thirty yolked oocytes from each ovary were measured. If the mean diameter of these oocytes was ≥0.86 mm, the fish was used in our fecundity estimates. Ovaries with advanced oocytes averaging <0.86 mm were considered not to be sufficiently mature to accurately identify the advanced stock of yolked oocytes (Hunter et al., 1992). Atretic oocytes were not included in our counts of advanced oocytes. The exclusion of atretic oocytes would not bias the computation of daily fecundity per female (D; eqn 1), as only 1.5% of advanced oocytes were atretic and the rate of atresia did not change with elapsed time.

Total fecundity (E) is the total number of advanced yolked and hydrated oocytes present in the ovary. Fecundity is determinate in Dover sole (Hunter et al., 1992) and decreases during the spawning season as advanced oocytes mature and are spawned. A linear regression was used to model the relationship between fecundity, fish weight, and day of the year (Fig. 3):

$$E = a_0 + a_w \cdot w + a_t \cdot t \tag{4}$$

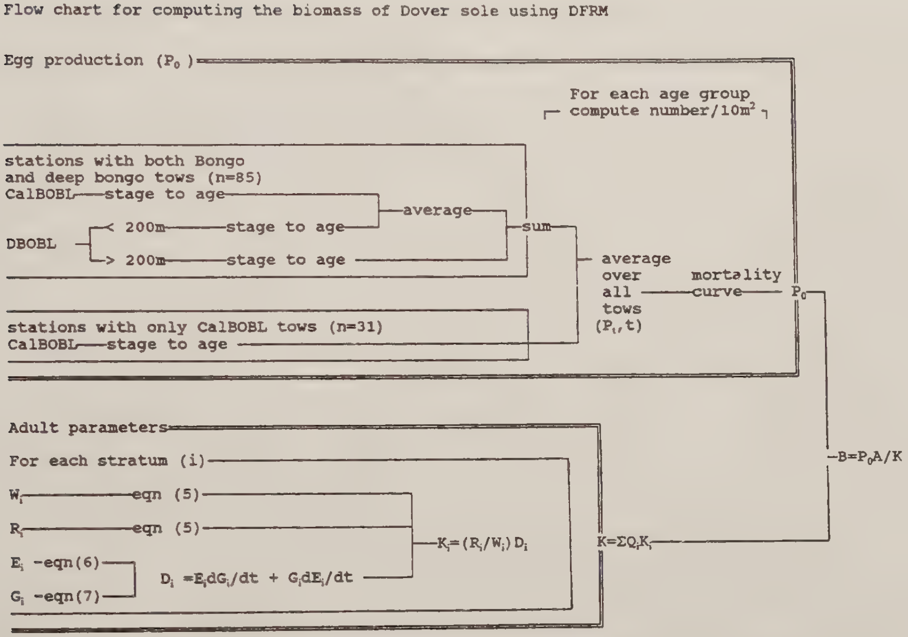
Flow chart for computing the biomass of Dover sole using DFRM
Egg production (P0)
For each age group compute number/10m²
stations with both Bongo and deep bongo tows (n=85)
CalBOBL—stage to age
average
DBOBL
< 200m—stage to age
> 200m—stage to age
sum
average over all tows (Pt, t)
mortality curve
P0
stations with only CalBOBL tows (n=31)
CalBOBL—stage to age
Adult parameters
For each stratum (i)
Wi—eqn (5)
Ri—eqn (5)
Ei -eqn(6)
Gi -eqn(7)
Di =EidGi/dt + GidEi/dt
Ki=(Ri/Wi) Di
K=ΣQiKi
B=P0A/K

Figure 3. Flow chart for computing the biomass of Dover sole using DRFM. (See Table 3).

where E is the fecundity, w is fish weight (g), and t is the day of the year (t; t = 1 for Jan 1, t = 2 for Jan 2, . . .).

FRACTION OF FEMALES WITH ACTIVE OVARIES (G). Ovaries from a subsample of up to 25 females from each trawl were examined on shipboard and assigned to one of three classes: *Hydrated,* translucent hydrated oocytes present; *Active,* yolked oocytes present; or *Inactive,* no yolked oocytes present. The fraction of females with active ovaries (G) was the number of active females plus the number of hydrated females, divided by the total number of females in the sample. After each cruise, the ovaries were reexamined and classified in the laboratory to determine the accuracy of the shipboard classification scheme. All ovaries were reexamined, but in 1988 only a subsample was reexamined. The results of these analyses indicated shipboard ovarian classification was reasonably accurate (91%; Hunter et al., 1992). To estimate the fraction of females with active ovaries in 1988, we converted deck-graded data to laboratory-graded (Appendix 1).

The fraction of females with active ovaries (G) would be expected to decline over the spawning season as females spawned. The fraction would also be expected to increase with weight since the attainment of sexual maturity is a function of female size. A Weibull distribution was used to model the relationship between the fraction of active females (G) and day of the year (t) (Hunter et al., 1992). Here, we chose to use a linear equation to obtain an overall decline rate of the fraction of females with active ovaries (G) with respect to female weight and day of the year within the survey period:

$$G = c_0 + c_w \cdot w + c_t \cdot t \tag{5}$$

From a theoretical standpoint, a nonlinear function may be a more suitable model for describing the annual decline of the fraction of females with active ovaries because the rate of decline in the proportion active decreases later in the season (Fig. 4). For the relatively short period under study, however, a linear model gave an adequate estimate of the average decline rate. The coefficient ($c_t = dG/dt$) for day of the year estimates the average decline rate of the fraction with elapsed time.

DAILY FECUNDITY PER FEMALE (D). The fecundity per female is the product of fecundity (E) and female fraction with active ovaries (G). Because both E and G decline during the season and females eventually spawn all of their advanced oocytes, at which time the ovary becomes inactive, the fecundity per female ($E \cdot G$) declines with time (t). The decline rate of $E \cdot G$ ($d(E \cdot G)/dt$) measures daily fecundity per female (Fig. 3) and can be expressed as

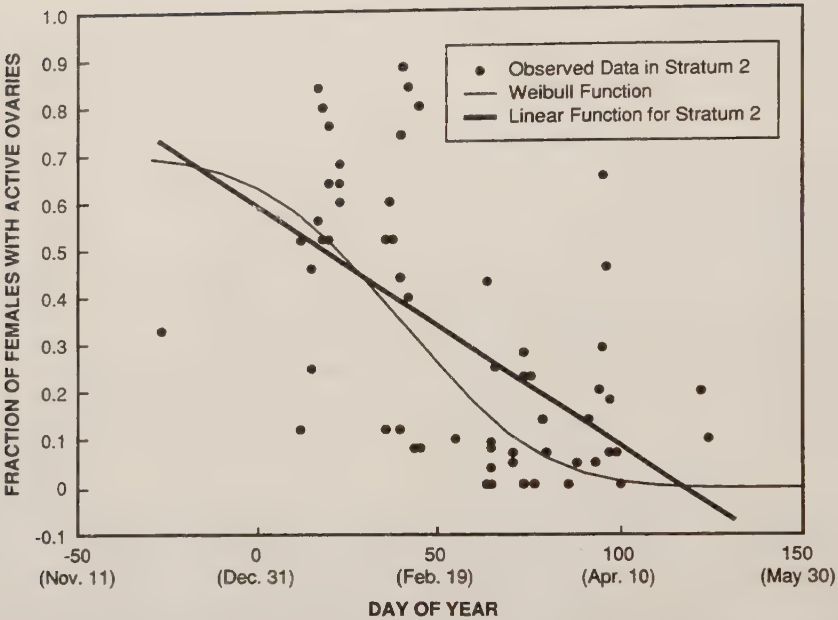

Figure 4. Fraction of females with active ovaries and day of year: Weibull distribution (Hunter et al., 1992) and linear function for stratum 2, 1985 to 1988.

$$D_t = d(E \cdot G)/dt$$

$$= E_t \cdot dG/dt + G_t \cdot dE/dt \qquad (6)$$

with approximate variance by the delta method (Appendix 2).

Daily Population Fecundity (K). To estimate the daily population fecundity of Dover sole, we computed the rate for each depth stratum (Fig. 3):

$$K = (R/W) \cdot D_{50} \cdot 10^6 \qquad (7)$$

The coefficient of variation of this rate [CV(K)] within each stratum (K) was computed by the delta method:

$$CV(K) = [CV(R)^2 + CV(W)^2 + CV(D_{50})^2 + 2 \cdot COV(D_{50}, R)/(R \cdot D_{50})$$

$$- 2 \cdot COV(R, W)/(R \cdot W) - 2 \cdot COV(D_{50}, W)/(D_{50} \cdot W)]^{0.5} \qquad (8)$$

The covariance terms, COV($D_{50}$, R) and COV($D_{50}$, W), were difficult to compute directly. Thus a bootstrapping method was used to estimate three covariance terms for each depth stratum.

Post-stratification of Survey Area by Depth. We stratified the survey area by bottom depth after the survey because adult parameters changed markedly with bottom depth (Hunter et al., 1990). Three depth strata were used: stratum 1 was area with bottom depth ≤249 fm (456 m), stratum 2 was 250 to 549 fm (457 to 1,004 m), and stratum 3 was ≥550 fm (1,005 m). Each reproductive parameter was computed for each stratum. An analysis of variance (ANOVA) or analysis of covariance (ANCOVA) was performed to test whether the differences in estimates among strata were statistically significant. The covariates were fish weight and day of the year. If estimates for different strata were different, the parameter estimates for each stratum were retained. If they were not different, data were pooled and the parameters were estimated using the pooled data. A complete set of adult parameter estimates was computed for each depth stratum even when the data from different strata were pooled to make the estimate. Each estimate from a stratum was weighted by the product of area covered by the stratum and the mean trawl catch for the stratum to arrive at an overall estimate. The weighted average for each individual parameter (X = R, W, $D_{50}$, and K) and its variance [V(X)] were computed

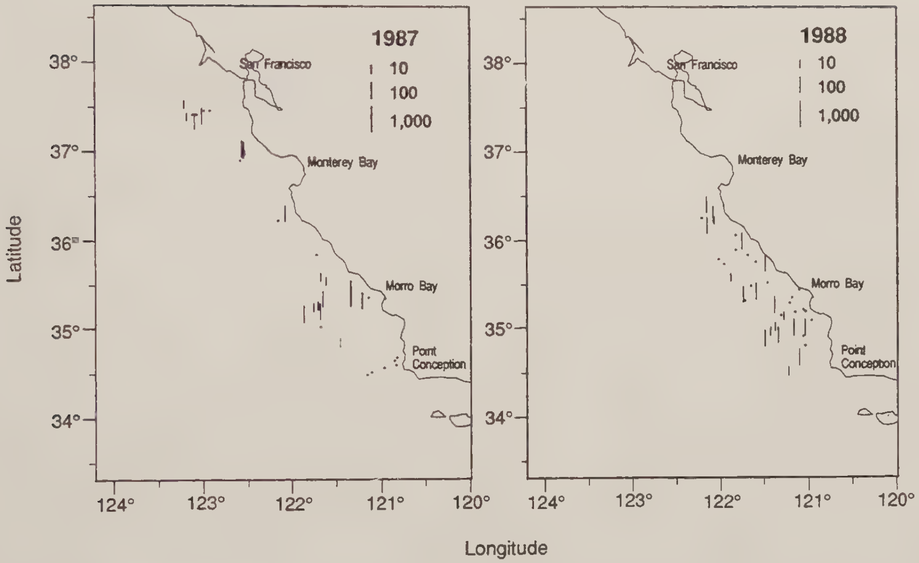

Figure 5. Spatial distribution of Dover sole eggs collected in DBOBL net in 1987 and 1988.

following standard procedures: $X = \Sigma Q_iX_i$ and $V(X) = V(\Sigma Q_iX_i) = \Sigma [Q_i^2V(X_i)]$ where $Q_i$ is the weight, $\Sigma Q_i = 1$ and $X_i$ is a parameter estimate in a stratum (Fig. 3).

## RESULTS

*Planktonic Egg Parameters.*—ESTIMATION OF DAILY EGG PRODUCTION ($P_0$). The eggs taken in each plankton tow (Fig. 5) were first converted to the numbers of eggs per 10 $m^2$ and then were grouped by their ages into daily age classes. We used the average number of eggs per 10 $m^2$ per age class over all stations to estimate the production rate, eggs spawned per day ($P_0$), and the daily egg mortality (z) (Fig. 3). Daily egg production was estimated for the survey area as a whole because eggs were transported between strata making stratification by depth impractical. Data from both CalBOBL and DBOBL were used in computing daily egg production.

The estimate obtained for the number of newly spawned eggs ($P_0$) was $2.10 \cdot d^{-1} \cdot 10\ m^{-2}$ (SE = 0.24) and the estimate of the mortality coefficient was $\beta = 0.63$ (SE = 0.06) (Fig. 6). The bootstrapped estimate of $P_0$ (1.94) was slightly lower than the direct computation. The standard error (0.58) of the bootstrapped estimate of $P_0$ was twice that from the regression. The bootstrapped estimate of the mortality coefficient was 0.65, similar to the direct computation, yet the standard error from the bootstrap method (0.13) was also twice the standard error computed from the direct computation (Table 3, Appendix 2).

*Estimation of Daily Population Fecundity (K).*—Estimates for parameters used to calculate daily population fecundity of Dover sole ($K = (R/W) \cdot D \cdot 10^6$; $eggs \cdot mt^{-1} \cdot day^{-1}$) are described below.

FEMALE WEIGHT (W). Average female weights for each stratum were used because ANOVA indicated that fish weights were significantly different among strata (F = 132.14, df = 2, 113). The mean female weight was 250.53 g (SE = 29.81 g,

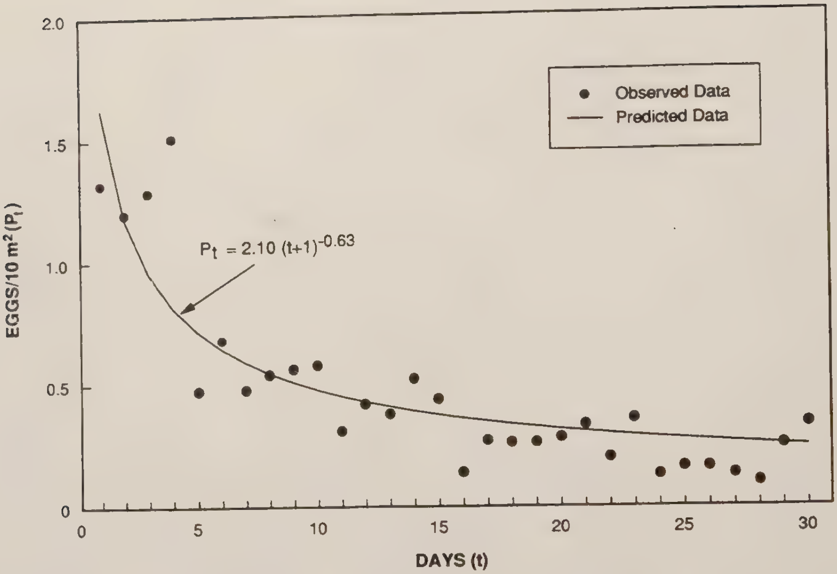

Figure 6. Dover sole egg mortality curve. Each point is the mean abundance per 10 m² by 1-day intervals.

N = 38) for stratum 1, 776.07 g (SE = 31.11 g, N = 62) for stratum 2, and 1,056.7 g (SE = 20.49 g, N = 16) for stratum 3. The weighted average female weight for the entire survey area was 668.51 g (SE = 25.06 g, N = 116), where the weighting factor was the product of stratum area size and mean catch from the swept trawls (Table 3). The standard errors of the estimates were obtained by the jackknife method (Efron, 1982) because the underlying distribution of the estimates was unknown. The bootstrapped estimates were similar to the direct computation, and the variances computed from the bootstrap method were also similar to the jackknife method (Table 3).

Female Fraction (R). We carried out an ANOVA to determine whether the female fractions were different among strata. The arcsine of the square root of sample ratios was used to normalize the female fraction in each trawl prior to the ANOVA. The results indicated that the female fractions in the three strata were significantly different from one another (F = 16.33; df = 2, 113; $P < 0.001$). Thus, we computed R for each stratum. The fraction (R) was 0.67 (SE = 0.034, N = 38) for stratum 1, 0.76 (SE = 0.031, N = 62) for stratum 2, and 0.92 (SE = 0.054, N = 16) for stratum 3 (Table 3). The weighted female fraction for the entire survey area was 0.74 (SE = 0.025, N = 116). The jackknife method was used to compute the standard errors of the estimates. Similar to the estimate of average female weight, the bootstrap method provided point estimates similar to the direct formula and variance close to the jackknife method (Table 3).

Total Fecundity (E). An analysis of covariance indicated that the regression coefficients for the day of the year for the three strata were similar (F = 0.55; df = 2, 245; $P = 0.58$) but the regression coefficients for fish weight were not the same among strata (F = 3.40; df = 2, 245; $P = 0.035$). The difference is due to the high value of regression coefficient in stratum 1 compared with the other two strata (Fig. 7). To accommodate these differences, we used two linear models for

Table 3. Estimates of parameters associated with adult reproduction of Dover sole, egg production ($P_0$), daily egg mortality coefficient ($\beta$), and biomass estimates (B and $B_c$) in central California by depth stratum, 1985 to 1988* (Sample size, N, is number of trawls)

| | Depth stratum (m; fm) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 0–456<br>0–249 | | 457–1,004<br>250–549 | | 1,005–1,280<br>550–700 | | Weighted mean† | |
| Method‡ | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 |
| W (g) | 250.53 | 253.22 | 776.07 | 763.7 | 1,056.7 | 1,063.5 | 668.51 | 659.5 |
| SE | 29.81 | 17.36 | 31.11 | 26.13 | 20.49 | 26.3 | 25.06 | 22.24 |
| N | 38 | 37 | 62 | 60 | 19 | 16 | | |
| R | 0.67 | 0.70 | 0.76 | 0.80 | 0.92 | 0.85 | 0.74 | 0.78 |
| SE | 0.034 | 0.023 | 0.031 | 0.023 | 0.054 | 0.07 | 0.025 | 0.02 |
| N | 38 | 37 | 62 | 60 | 16 | 16 | | |
| $D_{50} = d(E \cdot G) \cdot dt^{-1}$ | 100.38 | 145.93 | 288.60 | 282.93 | 463.52 | 451.03 | 250.82 | 255.84 |
| SE | 26.98 | 33.88 | 61.63 | 22.64 | 92.68 | 50.83 | 48.41 | 18.52 |
| N | 37 | 37 | 60 | 16 | 16 | | | |
| $K \cdot 10^{-6} = (R/W) \cdot D_{50}$ | 0.27 | 0.40 | 0.28 | 0.30 | 0.40 | 0.36 | 0.28 | 0.32 |
| CV | 0.30 | 0.23 | 0.18 | 0.07 | 0.21 | 0.14 | 0.15 | 0.09 |
| A (area, $km^2$) | 4,049 | | 7,204 | | 2,919 | | | |
| Mean catch $\cdot$ trawl$^{-1}$ (lbs) | 67.39 | | 140.14 | | 5.2 | | | |
| Weighting factor | 0.21 | | 0.78 | | 0.01 | | | |

| Method | 1 | 2 |
|---|---|---|
| $P_0 \cdot 10\ m^{-2}$ | 2.10 | 1.94 |
| SE | 0.24 | 0.57 |
| $\beta$ | 0.63 | 0.65 |
| SE | 0.06 | 0.13 |
| Stations§ | 116 | |
| B (mt) | 10,629 | 8,591 |
| CV | 0.19 | 0.31 |
| $B_c$ (mt) | | 12,567 |
| CV | | 0.38 |

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* Abbreviations are as follows: W, the average female weight (g); R, female fraction of the population by weight; E, the total fecundity for average female weight; G, the fraction of female with yolked eggs; $D_{50}$, the number of eggs spawned per female per day; $(R/W) \cdot D_{50}$, the daily population fecundity per gram; SE, standard error. The biomass estimate (B) was computed based on equation 1. $B_c$ is the bias-corrected biomass estimate.

† Weighted by the product of area and mean catch.

‡ Method 1 is the direct calculation from formulas described in the text. The standard error (SE) was based on regression estimate for $P_0$, jackknife estimates for R and W, and equation A3 for $D_{50}$. The CV of K was from equation 8. The SE of B was from equation 1A. Method 2 is the bootstrap method.

§ See Table 1 for number of CalBOBL and DBOBL tows.

fecundity: one for stratum 1 (depth ≤ 249 fm), and the other for strata 2 and 3 combined (depth ≥ 250 fm) (Table 4).

FRACTION OF FEMALES WITH ACTIVE OVARIES (G). We used an ANCOVA to determine if it was necessary to use a separate model for each of the three strata, where the covariates were female weight (W) and day of the year (t) and the arcsine of the square root was applied to the fraction (G). This analysis indicated that the active fraction of the same fish weight caught at the same day of the year was statistically different among strata (F = 6.13; df = 2, 108; *P* = 0.003), although the difference in slopes of two covariates among three strata were undetectable (F = 2.08; df = 4, 104; *P* = 0.08). As a result, a separate simple linear regression was obtained for each stratum (eqn 5). Our analyses indicated that female weight was an important variable in describing the fraction of females with active ovaries in stratum 2, but not in the other two strata. Thus, the fish weight was included as a variable only in stratum 2 (Table 4).

The overall decline rate of G was 0.0028, 0.0049, and 0.0056 per day for strata 1, 2, and 3, respectively. Except for stratum 1, these rates were similar to the

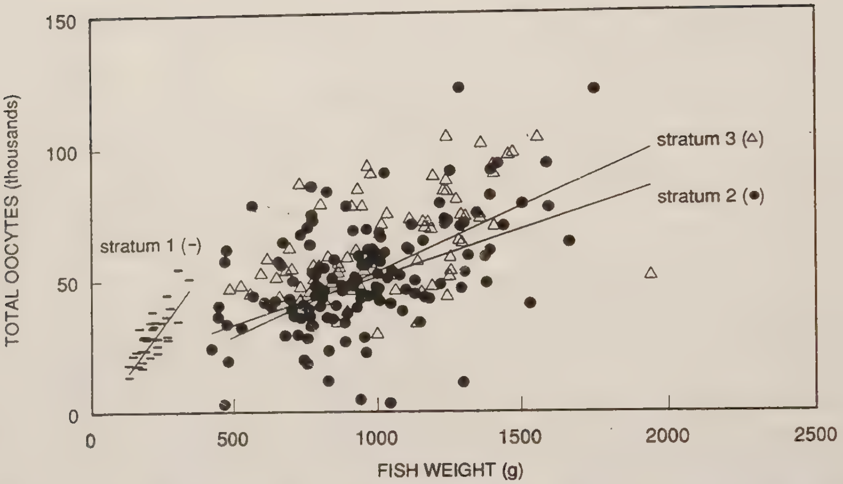

Figure 7. Linear relationship between total fecundity and body weight of Dover sole by depth stratum.

overall rate 0.005 per day computed from the Weibull function (Hunter et al., 1992; Fig. 4). Thus, the simple linear regression is a good approximation for the overall decline rate of G.

Because both E and G decrease as t increases, the mean daily fecundity per female (D) was estimated by $D_{50}$ at $t = 50$ (day of the year, say Feb 19), which was close to the middle of the study time period. The estimate of average daily fecundity per female for Feb 19, $D_{50}$, was 100.38 oocytes·female$^{-1}$·d$^{-1}$ (SE = 26.98, N = 37) for stratum 1, 288.60 (SE = 61.63, N = 60) for stratum 2, and 463.52 (SE = 92.68, N = 16) for stratum 3, where the sample size (N) was the number of trawls (Tables 3 and 5). The average value in each stratum was weighted by the product of the area and average catch per trawl of each stratum. The final estimate was 250.82 eggs spawned per female per day for all strata (Table 3). Except for stratum 1, the bootstrap estimates were similar to the estimates from the direct method and the bootstrapped variances were smaller than the direct computation (Appendix 2; eqn A3; Table 3). In stratum 1, the bootstrapped estimate was 40% higher than that from the direct formula.

DAILY POPULATION FECUNDITY (K). The last three terms in equation 8 were negligible within each stratum. Although our computation of CV(K) (=0.15) in-

Table 4. Linear regression of total fecundity (E) on female fish weight (W) and day of the year (t) and two functional relationships of fraction of females with active ovaries (G) on female fish weight (W) and day of the year (t) by depth stratum. N is number of fish for computing total fecundity (E), and is number of tows for computing G

| Stratum | Equation | N | $\sqrt{mse}$ | $R^2$ |
|---|---|---|---|---|
| | Total fecundity (E) | | | |
| 1 | $E = 1{,}334 + 146.53 \cdot W - 102.48 \cdot t$ | 32 | 5,677 | 0.63 |
| 2 + 3 | $E = 23{,}107 + 40.81 \cdot W - 237.5 \cdot t$ | 220 | 16,050 | 0.37 |
| | Fraction of females with active ovaries (G) | | | |
| 1 | $G = 0.22 - 0.0028 \cdot t$ | 37 | 0.152 | 0.28 |
| 2 | $G = 0.083 + 0.00064 \cdot W - 0.0049 \cdot t$ | 60 | 0.190 | 0.54 |
| 3 | $G = 0.945 - 0.0056 \cdot t$ | 16 | 0.257 | 0.47 |

Table 5. Summary of estimates of parameters used in estimating the number of eggs spawned per female per day ($D_{50}$ = $|d(E \cdot G)/dt|$), 1985 to 1988

| Parameter | Depth stratum (m; fm)<br>0–456<br>0–249 | 457–1,004<br>250–549 | 1,005–1,280<br>550–700 |
|---|---|---|---|
| $E_{50}$ | 32,920.16 | 42,903.42 | 54,355.93 |
| SE | 2,100.84 | 1,535.06 | 1,341.06 |
| dG/dt | −0.0028 | −0.0049 | −0.0056 |
| SE | 0.00075 | 0.00076 | 0.0016 |
| $G_{50}$ | 0.08 | 0.33 | 0.67 |
| SE | 0.027 | 0.031 | 0.078 |
| dE/dt | −102.48 | −237.5 | −237.5 |
| SE | 86.61 | 36.71 | 36.71 |
| COV(E, G)* | 133.53 | 1,130.66 | 235.26 |
| $D_{50}$ | 100.38 | 288.60 | 463.52 |
| SE | 26.98 | 61.63 | 92.68 |
| N (trawls) | 37 | 60 | 16 |

* $COV(E_t, G_t) = COV(a_0 + a_w \cdot W + a_t \cdot t, c_0 + c_w \cdot W + c_t \cdot t) = a_t \cdot c_t \cdot V(t)$ for a given fish weight (W) where, t is day of the year, $a_t$ and $c_t$ are regression coefficients of elapsed time (eqns 4 and 5). $E_t$ and $G_t$ are computed for the average fish weight in each stratum. For other abbreviations see Table 3.

cluded all covariance terms, CV(K) computed without covariance terms was 0.18 and thus should be acceptable.

Using equations 7 and 8, we obtained K = 0.27 × $10^6$ eggs·$mt^{-1} \cdot d^{-1}$ (CV = 0.30) for stratum 1, 0.28 × $10^6$ (CV = 0.18) for stratum 2, and 0.40 × $10^6$ (CV = 0.21) for stratum 3. The weighted average was 0.28 × $10^6$ (SE = 0.04 × $10^6$, CV = 0.15; Table 3). Similar to $D_{50}$, except for stratum 1, the bootstrapped estimates of K were close to the direct computation. In stratum 1, the bootstrapped estimate (0.4 × $10^6$) was higher than the direct computation (0.28 × $10^6$; Table 3). The bootstrapped estimate for the whole area (0.32 × $10^6$) was higher than the direct computation. The difference (0.04 × $10^6$) measures the bias of the estimate from the direct computation. Thus, the estimated K from equation 7 is biased upward. The variation of K was dominated by the variation of $D_{50}$ and the CV of K from the bootstrap method (0.09) was smaller than those computed from equation 8 (0.15; Table 3).

The rate of 0.28 × $10^6$ eggs·$mt^{-1} \cdot d^{-1}$, is much lower than the rate for northern anchovy which is 37 × $10^6$ eggs·$mt^{-1} \cdot d^{-1}$ in 1985 (Bindman, 1985). Thus, the daily spawning rate per unit weight of population of Dover sole is slightly less than 1/100th of the spawning rate per unit population of anchovy.

*Estimation of Biomass (B).*—The estimate of the biomass of Dover sole using daily fecundity reduction method was 10,629 mt (CV = 0.19; Table 3). The coefficient of variation of estimated biomass was computed without $COV(P_0 \cdot K)$ (eqn 1a) because $COV(P_0 \cdot K)$ cannot be estimated from the existing data set. The CV of B from the bootstrap method (0.31) was higher than that computed from equation 1a, primarily because of the high coefficient of variation of $P_0$ from the bootstrap method (Table 3). The bootstrapped estimate of biomass was 8,691 mt (Table 3). The bias-corrected estimate ($B_c$) was 12,567 mt (CV = 0.38; Appendix 2). Abundance estimates for Dover sole in the same study area using the swept trawl method in 1987 and 1988 range from 14,000 to 17,000 mt (Butler et al., 1989). Thus the daily fecundity reduction method estimate is close to the lower limit obtained by the swept trawl for the same area.

## DISCUSSION

We used an assortment of survey information taken over a number of years to estimate the biomass of Dover sole because data from one single year were inadequate to assess the population, although the bulk of the data were collected from 1987 and 1988. Moreover, the underestimation of biomass resulted from the fact that two requirements for the daily fecundity reduction method were not met fully: 1) the survey does not encompass the offshore limits of Dover sole eggs, and 2) the temperature history of the eggs was approximated for converting developmental stages of eggs to ages. The consequences of the problems, potential improvements, and future directions are discussed below.

*Bias Due to Egg Distribution.*—Our surveys covered a small fraction of the spawning area of Dover sole (Ahlstrom and Moser, 1975; Savage, 1989). For purposes of this demonstration, it can be assumed that the transport of eggs across the northern and southern boundaries of the survey area caused no bias because no obvious trend existed in their abundance along the coast (Fig. 5a, b). On the other hand, the density of eggs increases as one moves offshore. Surface tows taken with a MANTA net on the same cruises indicate that significant numbers of 1-day-old Dover sole eggs reach the top 16 cm of the sea surface. Assuming that at least some of these eggs originated at 1,000 m, where the spawning biomass is high (Hunter et al., 1990), we estimate that some of these eggs rose 1,000 m in 1 d or about 0.01 $m \cdot s^{-1}$. Such rapid vertical transport of eggs, coupled with long incubation periods of 30 d, would lead to considerable horizontal offshore transport of eggs. This suggestion is supported by the relatively high numbers of eggs found in samples near the outer edge of the Dover sole slope habitat. Thus, our calculation of total egg production may be considerably biased downward because eggs are likely to have drifted offshore from our survey area resulting in underestimation of A in equation 1.

Our estimate of $P_0$ may also be biased upward because older eggs are more likely to drift into the unsurveyed offshore area than are younger ones. This could cause an overestimate of egg mortality since the number of eggs per age class would be progressively underestimated with increasing age. An overestimate of egg mortality would cause an overestimate of $P_0$ since it is the extrapolated intercept of the egg mortality curve. If the mortality rate of Dover sole eggs was corrected for offshore transport of older eggs the actual rate would be less than 0.1 per day.

*Potential Egg Thermal History Bias.*—Surface temperatures were usually highest offshore and to the south in the study area. Thus, a more accurate estimate of spawning biomass of Dover sole will require additional information about water temperatures and the thermal history of eggs. Variability in water temperature, together with transport during the long incubation period, result in uncertainty about thermal history. In this regard, it may be useful to use eggs at ages up to 3 or 4 d in the computations to diminish the effects of transport and temperature change.

The incubation model and the vertical distribution used in this study are first approximations (Appendix 1). Additional data on Dover sole egg development rate over a range of temperatures, together with a quantitative study of the vertical distribution of their eggs in the water column, are essential for developing more precise models. We used the mean temperature over each of two depth ranges (depth $<200$ m, and depth $>200$ m) to assign ages to the eggs taken in each of these ranges. This method underestimates the age of the eggs in the upper depth range since the eggs are spawned at the bottom and rise through the lower range before reaching the upper one. Although, we believe the current method produces only a minor bias in the estimates of biomass, a temperature-dependent, vertical transit model for eggs would be preferable.

*Precision, Survey Design, and Vessel Requirements.*—A formal analysis of the precision of the daily fecundity reduction method for Dover sole is beyond the scope of this paper. Some information related to the design of sampling program is, however, available. The precision of daily population fecundity estimates (eggs spawned per gram of fish per day) depends on the decline rate of the fraction active (G) and total fecundity (E) during the spawning season, as well as on the number of trawl hauls containing adult Dover sole. Dover sole population fecundity (fraction of females with active ovaries) declines slowly during the spawning season (15% per month) consequently specimens must be collected over a rather long expanse of time to detect a time-dependent change in spawning rates. Our data indicate that 50 positive trawls (trawls in which some fish are caught) over a 100-d interval would provide an estimate of the daily rate of decline of the fraction active (G) with a coefficient of variation of 0.30. On the other hand, if the 50 positive trawls were taken over 30 to 40 d the coefficient for elapsed time is not detectable (CV = 2.50). Even if one doubled the number of trawls it is unlikely that an effect of elapsed time on G could be detected over a 40-d period because the coefficient of variation is so large. We reached similar conclusions for the detection of an effect of elapsed time on total fecundity (E). Thus, the most efficient survey design for Dover sole would be to sample the adults intermittently over 100 or more days. If a species had a much shorter spawning season and spawned fewer times than Dover sole, it would not be necessary to use such an extended survey design.

Estimation of $P_0$ for Dover sole may require fewer samples than are required for anchovy to achieve the same level of precision even though Dover sole eggs are less abundant than anchovy eggs. This is because the distribution of Dover sole eggs is less contagious than anchovy eggs. The percentage of tows that contains eggs of Dover sole (42%[1]) from both CalBOBL and DBOBL is higher than that for anchovy (36%, an average over 1987 to 1990) and the coefficient of variation for number of Dover sole per unit area (2.02) is lower than that of anchovy (2.50, an average over 1987 to 1990). To obtain a sample size for a given CV of $P_0$, we analyze data from DBOBL tows only. Our analysis indicates that the CV of $P_0$ ranges between 0.19 (eqn 2) and 0.37 (bootstrap method) from a total of 85 DBOBL tows (43 were positive) (Lo et al., 1992). We now take the worst case and accept 0.4 as the CV of $P_0$ from 85 DBOBL tows, then we will need total number of tows equal to $(0.4/CV)^2 \cdot 85$ for a desired CV of $P_0$. For example, for CV = 0.2, we need 340 DBOBL tows (172 positive stations), which is less than half of the tows required by anchovy (Bindman, 1985). The vertical distribution of eggs may be more variable than assumed in our analysis. If so, sample size may have to be considerably larger than 500.

If $P_0$ and K are measured simultaneously, a daily egg production estimate of fish biomass requires considerable ship time. Deep, quantitative plankton hauls (DBOBL) require much more time than standard CalBOBL tows (21.5 min for a 200-m standard CalBOBL tow versus about 2.5 h for 1,500 m), and 1-h trawl hauls require considerable time at the greater depths (1.2 h of ship time at 200 m versus 2.5 h at 1,500 m). Under ideal weather conditions, allowing only 1 h running time between stations, about 80 CalBOBL, DBOBL tows, and 1-h trawl hauls could be completed in 20 d, where the bathymetric depth range was 200 to 1,500 m and stations were made at 200-m depth increments. One alternative survey design to increasing the number of net tows for collecting Dover sole eggs would be to use less expensive shallow tows as the basic sampling units with occasional pairing of shallow tows with the DBOBL tows to provide an absolute calibration of shallow tows.

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[1] Out of 31 stations where only CalBOBL tows were taken, 3 stations were positive. Out of 85 stations where both CalBOBL and DBOBL tows were taken, 46 stations were positive.

*Comparison of Direct Method and Bootstrap Method Estimates.*—The biggest discrepancies between the direct computation and bootstrap method were the standard error of estimate of egg production for the whole area and the estimate of $D_{50}$ in stratum 1. The direct method seemed to underestimate $D_{50}$ in stratum 1 and the variance of $P_0$, and overestimate the variances of $D_{50}$ in strata 2 and 3, and thus in the whole area. The end result was that the biomass from the direct method was biased downward, and its variance was underestimated. The bootstrap method allowed a bias-corrected estimate by providing a measure of bias for the estimate of biomass from the direct method.

## CONCLUSION AND FUTURE DIRECTIONS

The daily fecundity reduction method is best suited to species having determinate annual fecundity and a relatively long spawning season, such as the Dover sole. the DFRM is preferred to the DEPM for Dover sole because of the difficulties in estimating spawning rates directly, due to the depth of their habitat and problems of calibrating estimates of the rate of spawning.

The DFRM is preferred to the AEPM owing to the long spawning season of Dover sole, and the relative high cost of the AEPM. The annual method requires ichthyoplankton surveys throughout the entire spawning season, whereas only a portion of the season needs to be surveyed if the DFRM is used. Even if the spawning season were short (1 to 2 months), several advantages may exist in using DFRM over using the annual method. The annual method requires an estimate of the potential annual fecundity and, in making this estimate, one must be certain that no spawning has taken place, that all oocytes considered to be the potential fecundity will actually be spawned, and that atretic losses of oocytes are minor (Hunter et al., 1992). In addition, assumptions may be required concerning the form of the annual egg production curve and the proportion of the year's annual production not covered by ichthyoplankton surveys. Neither the assumptions underlying estimates of annual fecundity nor those related to the annual egg production are usually evaluated. Since the DFRM requires fewer assumptions than the AEPM, it may be the preferable method even when spawning seasons are short.

Compared to trawl or acoustic surveys for estimating biomass, ichthyoplankton methods are usually more expensive but they provide more accurate estimates and require fewer assumptions if all key biological variables are measured in the current year. In trawl surveys, the catchability of fish is usually unknown, only relatively smooth bottoms can be trawled, and some pelagic species may be hopelessly undersampled by trawling. Acoustic surveys also have well known biases and assumptions. In the application of the DEPM to northern anchovy described in Lasker et al. (1985), all key biological variables were measured in the current year but, thus far, our work on DFRM has not achieved this level of accuracy. We lacked the extensive background of knowledge available for anchovy and were forced to make assumptions regarding incubation rates of Dover sole eggs, and based the estimate on the combined ichthyoplankton and gonad data from different years. Special problems were encountered in the application to Dover sole: quantitative plankton tows had to be taken from 1,500 m depth and adult reproductive activity and size varied with depth. These two problems were overcome and, after some current studies are completed, most of the assumptions affecting the accuracy of the method can also be eliminated. Since all parameters could be measured within a cruise, the DFRM has the potential of being as accurate as the DEPM.

In 1991, surveys were conducted to define the boundary of egg distribution, to obtain a good estimate of area A, and to collect data on the vertical distribution of eggs (Moser et al., in prep.). We are developing a temperature-dependent vertical transit model to refine the procedure for assignment of age to stage. In the future, we recommend simulation studies on estimates of biomass over a range of approximately 25 to 75 days rather than simply using $D_{50}$ as the best estimate of total biomass. Lastly, the final test of the method will be to carry out a DFRM survey in which all parameters are measured during the survey.

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## APPENDIX 1

### *Conversion Factors:*

*Standard Haul Factor (SHF).*—The SHF allows egg count to be expressed as number of eggs per 10 $m^2$ of sea surface area. The equation for the SHF is:

$$\mathrm{SHF} = 10 \cdot \mathrm{D}/(\mathrm{R} \cdot \mathrm{A} \cdot \mathrm{P})$$

where D is the depth of tow in meters, R is the number of revolutions of a flow meter in the mouth of the net, A is the area of the mouth of the net, and P is a flowmeter-specific calibration factor expressed in terms of the length (m) of the column of water needed to effect one revolution of the flow meter (Kramer and Ahlstrom, 1968). The depth of a CalBOBL tow is computed from the trajectory of the net, which is estimated from the cosine of the mean wire angle. The angle of the net is monitored at each 10 m of wire recovered.

In tows deeper than 200 m, wire angles do not provide accurate estimates of depth. To monitor the depth of DBOBL tows we attached a conductivity-temperature-depth (CTD) sensor to the net. The CTD records depth and water temperatures every 20 s. This allowed us to control the ship and winch speeds so that an approximately even volume of water was filtered at each depth. The equation that relates the tangent of the wire angle to the ship speed is:

$$V = V_0 \cdot \exp[r \cdot \tan(a)]$$

where, V is ship speed in $m \cdot s^{-1}$, $V_0$ is the intercept from a nonlinear least squares fit to the expected equation by the Marquardt algorithm, r is the exponential slope parameter, and tan(a) is the tangent of the wire angle in degrees. The estimates of parameters and their standard errors for the equation are $V_0 = 0.692$ (0.039) and $r = 0.271$ (0.037).

In practice, it was not possible to tow the net in an even trajectory to insure that every depth interval was sampled for the same amount of time on every tow. With a long towing wire, several minutes elapse before a net responds to a change in ship speed. In addition, undersea currents occasionally alter the angle of the towing wire. We believe, however, that no 10-m depth stratum was consistently over- or undersampled so that, on average, the entire water column was equally sampled.

*Length-weight Relationship.*—A single length-weight equation was applied to both sexes from 1,516 Dover sole taken in 1987 and 1988 because no differences between sexes were evident:

$$\ln(Y) = -14.07 + 3.43 \cdot \ln(X) + e$$

where Y is weight (g), X is total length (mm), and e is the error term with mean 0 and standard deviation $s = 0.1052$.

The model explained 98% of the variation in ln(Y) and there was no evidence of lack of fit. We used $\exp(-14.07 + 3.43 \cdot \ln(X) + e)$ to compute fish weight for a given length. For a nonlinear fit of the length-weight relation, see Hunter et al. (1992).

*Conversion from Deck-graded Ovaries to Laboratory-graded.*—To estimate the fraction of females with active ovaries in 1988, we computed rates of accuracy for the deck-grading based on a subsample of fish examined later in the laboratory for each of three legs of the 1988 cruise. For each leg, a contingency table was constructed as:

| | Laboratory | | | |
|---|---|---|---|---|
| Deck | Active | Inactive | Total | Rate of Accuracy |
| active | $m_{aa}$ | $ma_{ai}$ | $m_{a\cdot}$ | $p_a = m_{aa}/m_{a\cdot}$ |
| inactive | $m_{ia}$ | $m_{ii}$ | $m_{i\cdot}$ | $p_i = m_{ii}/m_{i\cdot}$ |

The first subscript refers to the deck grade and the second subscript refers to the laboratory grade; e.g., $m_{ia}$ is number of ovaries which were classified as inactive from deck examination and as active from laboratory examination. To obtain the corrected number of fish with active ovaries ($m_c$), we used the formula:

$$m_c = m_A \cdot p_a + m_I \cdot (1 - p_i)$$

where $m_A$ and $m_I$ are number of active female and inactive female from deck-grading for each trawl.

*Temperature-dependent Egg Development Model.*—We used two sets of incubation data to develop an algorithm for the assignment of ages to the 12 Dover sole egg stages: data from 111 Dover sole eggs incubated at 5.9°C (Table A1) and Apstein's (1909) hatching times of North Sea plaice, *Pleuronectes platessa,* at temperatures of 4 to 14°C (Table A2). The latter were used to approximate the relationship between temperature and time required to reach a stage (time-to-stage) for Dover sole because data were available for Dover sole at a single temperature (5.9°C). Incubation data for plaice eggs are a reasonable substitute for those of Dover sole because the diameter of the yolk mass is similar (ca. 2 mm) in the two species, and their eggs incubate in the water column over a similar temperature range, although Dover sole egg development is much slower than plaice at 6°C.

A relationship between temperature and time-to-stage for Dover sole was derived from the relationship between hatching time and temperature for plaice

$$h(T) = 45.06 \cdot \exp(-0.123 \cdot T) \tag{A1}$$

where h(T) is hatching time in days and T is temperature in °C (Apstein, 1909). Because the incubation period of Dover sole is longer than plaice at 6°C, we applied only the temperature coefficient of hatching time of plaice (eqn A1) to estimation of development rate of Dover sole eggs.

If one assumes that the proportional change in time-to-stage for Dover sole over a wide range of temperatures is the same as the proportional change in the time to hatching for plaice, then

Table A1. Mean, standard deviation (SD) and coefficient of variation (CV) of time-to-stage (days) for Dover sole eggs from 1987 experiment at 5.9°C; N is number of eggs sampled (Values in parentheses are guessed values)

| Stage | N | Mean | SD | CV |
|---|---|---|---|---|
| I | | (0.5)* | | |
| II | 38 | 0.955 | 0.383 | 0.40 |
| III | 9 | 3.288 | 0.575 | 0.17 |
| IV | 6 | 5.067 | 0.418 | 0.08 |
| V | 21 | 6.633 | 0.551 | 0.08 |
| VI | 18 | 9.856 | 1.072 | 0.10 |
| VII | 2 | 14.40 | (1.4) | (0.10)† |
| VIII | 0 | — | — | — |
| IX | 4 | 17.40 | (1.7) | (0.10)† |
| X | 7 | 22.29 | 1.513 | 0.070 |
| XI | 4 | 25.50 | 2.00 | 0.08 |
| XII | 2 | 28.5 | (2.28) | (0.08)† |

* 0.5 is the rounded off midpoint of 0 and 0.955.

† The CV of stage VI was used for stages VII and IX. The CV of stage XI was used for stage XII.

$$
\begin{aligned}
t_s(T) &= t_s(5.9)\cdot h(T)/h(5.9) \\
&= t_s(5.9)\cdot \exp(-0.123\cdot T)/\exp(-0.123\cdot 5.9) \\
&= t_s(5.9)\cdot \exp[-0.123(T - 5.9)] \qquad \text{(A2)}
\end{aligned}
$$

where $t_s(T)$ is the time-to-stage for Dover sole in days at temperature T°C. For example, at 10°C, the time to stage 5 is $t_5(10) = 6.633\cdot\exp[-0.123\cdot(10 - 5.9)]$, or $6.633\cdot 0.604 = 4.0$ d (Table A1).

*Allocation of Staged Eggs from DBOBL to Two Depth Segments.*—Dover sole eggs experience a wide range of incubation temperatures. Eggs are spawned at the bottom, where temperatures average about 3°C, and then rise in the water column, some reaching the surface where temperatures average 13°C. In order to assign ages to staged eggs, it was necessary to estimate the average temperature experienced by the eggs prior to capture. The water column was divided into two segments: from the bottom to 200 m and from 200 m to the surface. The average mid-depth temperature for the upper segment (<200 m) was 10.3°C (N = 77, SD = 0.49) and for the lower segment (>200 m) was 6.2°C (N = 76, SD = 0.93) (Table A3).

We used mid-depth temperatures at each station in equation A2 to compute the duration of each egg stage although the exact location and thermal history of individual eggs within a water column segment were unknown. The average mid-depth temperature within a stratum was used when no temperature was recorded for a station.

To assign the appropriate number of eggs taken in the DBOBL to each of the two water column segments, we computed a proration coefficient (pc) to be the ratio of number of eggs per 10 m² taken in the CalBOBL to that taken in the DBOBL for each stratum. We assumed that at each station both nets swept through the same group of eggs. The ratio was computed for each of three strata, at all the ichthyoplankton stations in which at least one of the two nets contained one or more eggs. The ratio for all positive stations was 1.0 (N = 11) for stratum 1, 0.5 (N = 53) for stratum 2 and 0.34 (N = 21) for stratum 3. Thus, in stratum 1, the catch of DBOBL was the same as that of CalBOBL. In stratum 2, the CalBOBL only catches half of the eggs in the water column, whereas in stratum 3, close to ⅓ of the eggs in the water column was caught by the CalBOBL.

We allocated staged eggs per 10 m² taken in each DBOBL tow into upper and lower segments of the water column using the following procedure for each stratum:

Table A2. Hatching time (days) of North Sea plaice at temperatures (T) between 2° to 24°C (Apstein, 1909). Estimated values were computed by using the exponential function $y = 45.06\cdot\exp(-0.123\cdot T)$

| Hatching time (d) | Temperature (°C) | | | | | | |
|---|---|---|---|---|---|---|---|
| | 2 | 4 | 6 | 8 | 10 | 12 | 14 |
| Observed | 37 | 26 | 20 | 16 | 13 | 11.5 | 10 |
| Estimated | 35.2 | 27.5 | 21.5 | 16.8 | 13.15 | 10.28 | 8.04 |

Table A3. Mean, standard deviation (SD) of water temperature, and estimated hatching time, and the proration factor for time-to-stage at the surface, mid-depth of water column <200 m, and mid-depth of water column >200 m, off central California, 1987 to 1988 (N is number of tows)

| | | Mid-depth | |
|---|---|---|---|
| | Sea surface | <200 m | >200 m |
| Water temperature (°C) | | | |
| Mean | 13.03 | 10.27 | 6.2 |
| SD | 0.756 | 0.493 | 0.929 |
| N | 116 | 77 | 76 |
| Hatching time (d) | 11.9 | 16.05 | 27.30* |

* 27.30 = 28.50·exp[0.123·(6.2 − 5.9)].

1. $N_u = N \cdot pc$
2. $N_{ui} = N_u \cdot B_i,$ $\quad i = 1, \ldots, 12$
3. $N_{ui} = N_i,$ $\quad$ if $N_{ui} > N_i$
   $N_{ui} = N_{ui},$ $\quad$ if $N_{ui} < N_i$
4. $N_{Li} = N_i - N_{ui}$

where N is the total number of eggs per 10 m² in the DBOBL; pc is the proration coefficient computed for each stratum; $N_u$ is the total number of eggs per 10 m² allocated to the upper level, and was computed as a binomial random variable with parameters N and pc; $N_i$ is the number of eggs of the ith stage per 10 m² in DBOBL; $B_i$ is the fraction of eggs of the ith stage in the CalBOBL net; and $N_{ui}$ ($N_{Li}$) is the number of eggs per 10 m² of the ith stage allocated to the upper (lower) level.

Step 3 states that if the number of eggs of stage i in DBOBL was fewer than the number of eggs allocated to the upper 200 m, then all the eggs of stage i would be allocated to the upper 200 m. At few stations, either $N_{ui}$ or $N_i$ was zero, then no egg of stage i was allocated to the upper 200 m.

After the eggs caught in DBOBL tows were allocated to each of two segments, the actual age of eggs was then determined according to their developmental stages and the water temperature by a normal distribution. The mean is the average time to reach the stage and the standard deviation is the product of the CV and average time-to-stage where, CV for time-to-stage at 5.9°C was used for all temperatures (Table A1).

## Appendix 2

*Variance of $D_t$.*—

$$\begin{aligned} V(D_t) = {} & V(E_t)\cdot(dG/dt)^2 + V(dG/dt)\cdot(E_t)^2 + 2E_t\cdot(dG/dt)\cdot COV(E_t, dG/dt) \\ & + V(dE/dt)\cdot Gt^2 + V(G_t)\cdot(dE/dt)^2 + 2\cdot G_t\cdot(dE/dt)\cdot COV(G_t, dE/dt) \\ & + 2\cdot COV(E_t\cdot dG/dt, G_t\cdot dE/dt) \\ = {} & V(E_t)\cdot(dG/dt)^2 + V(dG/dt)\cdot(E_t)^2 + V(dE/dt)\cdot G_t2 + V(G_t)\cdot(dE/dt)^2 \\ & + 2\cdot(dG/dt)\cdot(dE/dt) + COV(E_t, G_t) \end{aligned} \tag{A3}$$

In equation (A3), $E_t$ and $G_t$ were computed from equations 4 and 5, respectively, for average female weight and t = 50, the midpoint of the survey. The daily rates, dG/dt and dE/dt, were estimated by separate regressions so that $COV(E_t, dG/dt)$ and $COV(G_t, dE/dt)$ can be assumed equal to zero. The term $COV(E_t\cdot dG/dt, G_t\cdot dE/dt)$ is reduced to $(dG/dt)\cdot(dE/dt)\cdot COV(E_t, G_t)$, and $COV(E_t, G_t)$ was computed by $a_t \cdot c_t \cdot V(t)$ for a given average female weight (eqns 4 and 5), while other covariances were zero when the linear regression coefficients were used for dG/dt and dE/dt.

*Parameter Estimates from the Bootstrap Method.*—The bootstrap resampling procedure was carried out for plankton and adult samples separately. Bootstrapped point estimate and coefficient of variance were obtained. Covariance was computed for the adult parameter estimates. The bias of biomass was estimated and was used to reduce the bias of biomass computed directly from equation 1.

*Daily Egg Production ($P_0$) and Daily Instantaneous Mortality Coefficient ($\beta$).*—We bootstrapped the data set of 116 stations, where CalBOBL tows were taken at 31 stations and both CalBOBL and DBOBL tows were taken at 85 stations. Each of the 116 records contains number of eggs per 10 m² in 12 stage categories for each net type. One single iteration included a random sample of 116 records (tows) with replacement from the original data set. The egg production ($P_0$) and mortality coefficient ($\beta$) were computed following the procedures described in Results section. From 500 iterations, the point estimate of $P_0$ was the mean of 500 bootstrapped values for $P_0$, and the coefficient of variation of $P_0$ was computed as the standard deviation of 500 bootstrapped values for $P_0$ divided by the mean of those values.

*Adult Parameters.*—These include: the fraction of the population being female (R), average female weight (W), daily fecundity per female ($D_{50}$), and daily population fecundity (K).

Two data files were extracted from 1985 to 1988 adult fish data sets to be bootstrapped for the point estimate and the CV of R, W, $D_{50}$, and K. Data required to compute R, W, and fraction of females that have active ovaries (S) are contained in one data file, and data required to compute weight-specific fecundity (E) are contained in a separate data file. Both data files contain year and haul number for cross reference. In the first data file, each record contains sample data: sampled total female weight, number of females, sample weight, number of fish in the sample, number of females with active ovaries and number of females with inactive ovaries, depth of the two, day of the year, and year-haul number. In the second data file, each record contains fecundity information of one individual fish: number of yolked eggs, fish weight, and depth of tow, year-haul number, and total number of fish sampled for fecundity for each haul.

The bootstrapping procedures are as follows. For each stratum, a fixed number of tows was selected randomly with replacement for the first data file and the number of tows was the minimum number used for all adult parameters (Table 3): 37 for stratum 1, 60 for stratum 2, and 16 for stratum 3. Any one selected tow was further checked to see if there was any fish sampled for fecundity, i.e., whether there was a record of the same year-haul number in the second data file. If so, from the second data file and within the year-haul number, fish were selected with replacement and the sample size was the original number of fish sampled for fecundity. Otherwise, the resampling process was continued. The total number of fish bootstrapped for each stratum was equal to the actual number of fish sampled in 1985 to 1988: 32 for stratum 1, 141 for stratum 2, and 79 for stratum 3. Within each such iteration, R, W, S, E, $D_{50}$, and K were computed according to the formula given in the Methods and Materials section. A total of 500 iterations was run and the point estimate and the CV for each parameter estimate was computed. The covariance of any two of R, W, $D_{50}$, and K wa also computed.

*Estimate of Biomass (B).*—For each of 500 iterations, the biomass was computed (eqn 1). The point estimate of biomass and its CV were obtained as done for other parameters. The bias of biomass estimate was computed as the difference between the bootstrapped point estimate ($B_b$) and the biomass estimate (B) directly computed from equation 1. A bias-corrected biomass estimate ($B_c$) is:

$$B_c = B - (B_b - B)$$

with variance

$$V(B_c) = 4 \cdot V(B) + V(B_b).$$

MACEWICZ AND HUNTER: SPAWNING FREQUENCY AND BATCH FECUNDITY OF *T. SYMMETRICUS*
CalCOFI Rep., Vol. 34, 1993

# SPAWNING FREQUENCY AND BATCH FECUNDITY OF JACK MACKEREL, *TRACHURUS SYMMETRICUS*, OFF CALIFORNIA DURING 1991

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## ABSTRACT

In southern California waters, during March–April 1991, the average mature female jack mackerel, *Trachurus symmetricus*, spawned every 5 days, and eight percent of the females spawned at 1–3 day intervals. The average relative batch fecundity was 112 oocytes per gram female weight (without ovary). Batch fecundity was lower for females that had spawned within the last 3 days than for females in which no evidence existed for a previous spawning.

## RESUMEN

En aguas de California sur, durante Marzo–Abril de 1991, los especímenes maduros promedio del charrito (*Trachurus symmetricus*) desovaron cada 5 días; ocho porciento de las hembras desovó en intervalos de 1–3 días. La fecundidad relativa promedio por cada puesta fué de 112 ovocitos por gramo (peso corporal de hembra libre de ovarios). La fecundidad por cada puesta en las hembras que habían desovado en los últimos 3 días fué menor que en las hembras en las que no se observó evidencia de desove previo.

## INTRODUCTION

Jack mackerel, *Trachurus symmetricus* (Ayres, 1855), range from Baja California to the Gulf of Alaska and from coastal waters up to 1000 miles offshore (MacCall and Stauffer 1983). The southern California fishery usually takes fish 10–30 cm (FL, fork length). No fishery presently exists for larger fish (FL >40 cm), which occur predominantly offshore and to the north (MacCall et al. 1980; MacCall and Stauffer 1983; Mason 1991). The potential value of an offshore trawl fishery for *T. symmetricus* has attracted some interest lately, and if such a fishery were to develop, estimates of *T. symmetricus* biomass from California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton data would be a valuable management tool.

MacCall and Stauffer (1983) used CalCOFI data and reproductive information on *T. symmetricus* to estimate the average biomass off western North America. Their chief barrier for estimating a time series of *T. symmetricus* biomass from CalCOFI data was the lack of information on daily rates of spawning (spawning frequency) and numbers of oocytes released per spawn (batch fecundity). The object of this paper is to provide new estimates of these two reproductive parameters for *T. symmetricus*.

Relatively little is known about the reproductive biology of *T. symmetricus* from the California Current. Gonad development and sexual maturity were studied by Wine and Knaggs (1975), and some preliminary fecundity estimates are available in MacGregor (1976). Lisovenko and Andrianov (1991) estimated the spawning frequency of *Trachurus murphyi* from Peruvian waters. Other works related to reproduction of *Trachurus* include various analyses of CalCOFI ichthyoplankton data to estimate the seasonality of reproduction, diel time of spawning, and distribution of eggs and larvae (Ahlstrom and Ball 1954; Farris 1961; Kramer and Smith 1970; Moser et al. 1993). Temperature-specific egg incubation rates are also known for *T. symmetricus* (Zweifel and Lasker 1976).

## METHODS

Jack mackerel, *Trachurus symmetricus*, were collected about 200 nautical miles off the southern California coast (figure 1) from March 23 to April 9, 1991, during a cooperative cruise on the R/V *Novodrutsk* (from Vladivostok, Russia). A large, nearly square, pelagic trawl with a vertical and horizontal opening of 75–80 meters was towed at 4.2 to 5.5 knots to collect the fish. Most of the 36 trawls were made at night; they lasted from 50 minutes to 8 hours and 40 minutes (Macewicz and Abramenkoff 1993). Surface water temperature ranged from 13.5°C to 14.7°C.

*T. symmetricus* were randomly sampled from the catch. Up to 100 fish from each haul were sexed, and measured (FL) to the nearest millimeter; their gonads were also classified (Macewicz and Abramenkoff 1993). From each trawl, 5 to 22 females were selected, not on the basis of maturity, but at random. The females were individually weighed (to the nearest gram) and their ovaries were removed and pre-

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[Manuscript received February 1, 1993.]

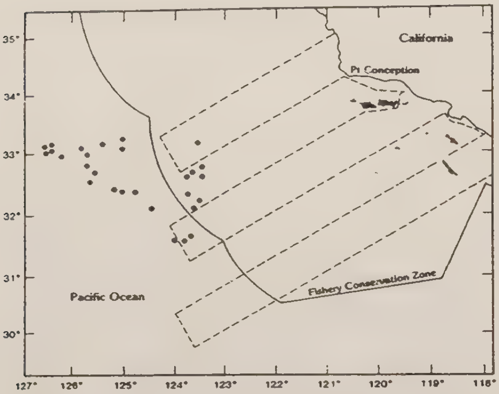

Figure 1. Location of the jack mackerel survey during March 23–April 9, 1991. *Circles* = trawls in which *Trachurus symmetricus* were taken; *dotted line* = the CalCOFI survey pattern.

served in 10% neutral buffered Formalin. Analysis of the preserved ovaries of these female *T. symmetricus* is the subject of this paper.

### *Histological Classification*

The preserved ovaries were weighed to the nearest milligram in the laboratory. A piece of each ovary was removed, dehydrated, and embedded in Paraplast. Histological sections were later cut at 5–6 µm and stained with Harris hematoxylin followed by eosin counterstain (H&E).

Each ovary was classified histologically in the manner developed for northern anchovy, *Engraulis mordax*, by Hunter and Goldberg (1980) and Hunter and Macewicz (1985a,b) with a few modifications for the ovarian structure of *T. symmetricus*. Oocytes in *T. symmetricus* ovaries develop asynchronously; that is, oocytes in many stages of development occur simultaneously in reproductively active ovaries (Wallace and Selman 1981). In each ovary we recorded the presence or absence of the following characters: oocytes that had not begun vitellogenesis; oocytes in early vitellogenic stages (0.28–0.54 mm in diameter); advanced yolked oocytes (smallest about 0.42 mm in diameter) in which any stages of nucleus migration (precursor to hydration) or hydration (>0.95 mm in diameter) were noted; and postovulatory follicles.

Unlike the developing oocytes of northern anchovy, those of *T. symmetricus* contain lipid droplets. The lipid first appears in oocytes about 0.19 mm in diameter (before vitellogenesis starts) and then eventually surrounds the nucleus and begins to fuse. Just before the nucleus migrates, partially fused lipid droplets begin moving to the side of the nucleus opposite the direction of migration. This location of the oil droplets on one side of the nucleus is a unique character that signals the onset of the migratory-nucleus stage. For this reason, oocytes in the migratory-nucleus stage can be detected much earlier in *T. symmetricus* than in species lacking an oil droplet, such as the northern anchovy.

Ovarian atresia in most teleosts seems to follow a similar sequence of stages (α, β, γ, and δ), as defined by Bretschneider and Duyvene de Wit 1947; Lambert 1970; and Hunter and Macewicz 1985b. We examined the ovarian sections for the presence of alpha (α) atresia of yolked oocytes and grouped them as follows: none, α < 50% (1 oocyte to 49% of the yolked oocytes were in α atresia), or α ⩾ 50% (50% or more of the yolked oocytes were in α atresia). The presence of beta (β) atresia was also noted. Alpha atresia of *T. symmetricus* was essentially similar to that described and illustrated for northern anchovy by Hunter and Macewicz (1985b); however, β atresia in *T. symmetricus* differed from northern anchovy because numerous vacuoles were scattered between the follicle cells. The vacuoles are probably remnants of the lipid droplets, which take longer than yolk to resorb, and in H&E slides appear empty. Ovarian atresia may indicate that the end of a spawning season is approaching (Hunter and Macewicz 1980, 1985b).

### *Spawning Frequency*

To measure spawning rate from postovulatory follicles, one must be able to estimate the age of the postovulatory follicles on the basis of their deterioration (Hunter and Goldberg 1980; Hunter and Macewicz 1985b). The best way to develop criteria for estimating the age of postovulatory follicles is to spawn fish in the laboratory and sample at known times after spawning. Alheit et al. (1984) were able to estimate age of postovulatory follicles for *Engraulis ringens* by sampling fish at sea through the day and night. They then reconstructed the degeneration rate of the postovulatory follicles by analyzing the time series. This alternative method requires a diel rhythm of spawning so that the elapsed time from spawning to capture can be used to assign ages to postovulatory follicles. Farris (1961) demonstrated that *T. symmetricus* spawn only at night, with a peak around midnight, which indicates that the method of Alheit et al. is possible.

It was not practical for us to spawn *T. symmetricus* females in the laboratory, so we used the method of Alheit et al. (1984). We used the time of day of the trawls (table 1) to estimate the age of *T. symmetricus* postovulatory follicles. Although some gaps existed in the time series (0600–1200 and 1500–2000), we were able to discriminate between postovulatory follicles 0–6 h old, 12–30 h old, 36–54 h old, and older than 60 h. Because degeneration and resorption of postovulatory follicles is a continuous process, we estimated ages based on the extent of changes in the following: the size and apparent shape of the follicle (from large and convoluted to V-shaped and 1/10 of the original size); appearance of the granulosa cells (from many healthy cells with nuclei linearly arranged, to a few cells containing pycnotic nuclei, cytoplasmic vacuoles, and granules); appearance of the lumen; and the size of the thecal layer. The histological characteristics are very similar to those described for *Scomber japonicus* (Dickerson et al. 1992) and northern anchovy (Hunter and Goldberg 1980; Hunter and Macewicz 1985a).

### *Batch Fecundity*

Batch fecundity (*F*, number of oocytes per spawn) was considered to be the number of oocytes in the ovary that either contained migratory nuclei or were hydrated. We used the gravimetric method (Hunter et al. 1985, 1992) to estimate the mean number of such oocytes that each ovary contained. Dioses et al. (1989) showed that location of tissue samples does not affect estimates of batch fecundity in *T. murphyi*, which indicates that such oocytes are dispersed randomly throughout the ovary. We teased apart oocytes in a few drops of 50% glycerin and then identified, counted, and measured them, using a digitizer linked by a video camera system to a dissection microscope. Hydrated ovaries containing new postovulatory follicles were not used to estimate batch fecundity.

TABLE 1

**Number of Mature Female Jack Mackerel, *Trachurus symmetricus*, from Trawl Samples Taken off Southern California in 1991**

| Trawl number | Date | | Trawling midpoint hour | Mature females | | |
|---|---|---|---|---|---|---|
| | Mo | Day | | Total | Non-spawn | Spawn[*] |
| 1 | 03 | 23 | 1500 | 11 | 5 | 6 |
| 2 | 03 | 23 | 2000 | 20 | 12 | 8 |
| 3 | 03 | 24 | 2400 | 18 | 10 | 8 |
| 6 | 03 | 25 | 2000 | 20 | 5 | 15 |
| 7 | 03 | 25 | 2400 | 20 | 6 | 14 |
| 8 | 03 | 26 | 1400 | 21 | 3 | 18 |
| 9 | 03 | 26 | 2100 | 10 | 2 | 8 |
| 10 | 03 | 27 | 0300 | 10 | 0 | 10 |
| 11 | 03 | 27 | 2200 | 20 | 2 | 18 |
| 13 | 03 | 28 | 2100 | 21 | 6 | 15 |
| 15 | 03 | 29 | 2100 | 20 | 5 | 15 |
| 17 | 03 | 30 | 2000 | 19 | 4 | 15 |
| 18 | 03 | 31 | 2400 | 21 | 3 | 18 |
| 19 | 03 | 31 | 2000 | 20 | 2 | 18 |
| 20 | 04 | 01 | 0100 | 10 | 0 | 10 |
| 22 | 04 | 01 | 2000 | 20 | 4 | 16 |
| 23 | 04 | 02 | 0300 | 5 | 0 | 5 |
| 24 | 04 | 02 | 2000 | 5 | 0 | 5 |
| 26 | 04 | 03 | 0600 | 10 | 3 | 7 |
| 27 | 04 | 03 | 2200 | 22 | 12 | 10 |
| 28 | 04 | 05 | 2200 | 21 | 8 | 13 |
| 29 | 04 | 06 | 1200 | 6 | 5 | 1 |
| 31 | 04 | 07 | 0200 | 5 | 5 | 0 |
| 32 | 04 | 07 | 2100 | 18 | 10 | 8 |
| 33 | 04 | 08 | 0400 | 10 | 5 | 5 |
| 34 | 04 | 08 | 2100 | 20 | 12 | 8 |
| 36 | 04 | 09 | 2400 | 10 | 8 | 2 |
| All | | | *N* | 413 | 137 | 276 |
| | | | % | | 33 | 67 |

[*] Sum of the females identified as having spawned in the last 54 hours or as able to do so within 24 hours.

In Formalin-preserved material, migratory-nucleus-stage and hydrated oocytes are easily identified. Hydrated oocytes are very large and translucent, with faint segmentations resulting from the fusing of yolk globules into "large plates." Oocytes with late-stage migratory nuclei are larger and less opaque than the other yolked oocytes and have a wide, clearish band on the periphery resulting from fusing of some yolk globules. In addition, a reflective oil drop (or several if lipid droplets are still fusing) is prominent in the migratory-nucleus and hydrated-oocyte stages. Oocytes at the migratory-nucleus stage are detectable in whole oocyte material only after most of the lipid droplets have come together and begun to fuse. Early stages of the movement and fusion of lipid droplets in migratory-nucleus oocytes can be accurately identified in histological sections, but in whole oocytes the early stages are difficult to see. Our examination of the ovaries of 42 females (33 in which the migratory-nucleus stage was distinct, and 9 in which it was difficult to see) indicated that the stage could be consistently detected when the mean diameter of the migratory-nucleus-stage oocytes was 0.69 mm or larger. This detection criterion may, however, be different for other microscope imaging systems. Only when the migratory-nucleus-stage oocytes averaged 0.69 mm or larger did we use them to estimate batch fecundity.

To compare the number and size of oocytes in the spawning batch to the other oocytes in the ovary, we measured oocyte size-frequency distributions in three females. We measured about 200 oocytes, and identified them by four developmental stages:

1. unyolked but with lipid droplets
2. early yolking
3. advanced yolked
4. about to be spawned—hydrated or with migrating nuclei

We counted the rest of the oocytes in the weighed subsample by stage. For ovaries with oocytes in stages 3 and 4, we measured 30–50 oocytes in each stage, and counted the remaining in each stage.

We estimated the batch fecundity of 33 females: 6 on the basis of counts of hydrated oocytes, and the rest on counts of migratory-nucleus-stage oocytes. In all, 40 females with ovaries containing hydrated oocytes were collected, but 34 of these had ovaries containing new postovulatory follicles, which indicated that they had just begun to spawn and thus were not suitable to be used for estimating batch fecundity.

## RESULTS

### *Spawning Frequency*

Of the 415 female jack mackerel ovaries collected and preserved, 413 were histologically classed as mature because they had ovaries containing yolked oocytes or beta atresia. Two females (one from trawl 11 and one from trawl 36) were classed as immature because their ovaries contained no yolked oocytes and no stages of atresia. The ovaries of 67% of the mature females contained postovulatory follicles (≤54 hours old), or hydrated oocytes, or migratory-nucleus-stage oocytes, indicating that these females had spawned within the last 54 hours or would do so within the next 0–24 hours (table 1).

Spawning frequency was calculated on the basis of histological evidence of three different nights:

*Spawned on night of capture*: late migratory-nucleus-stage oocytes, hydrated oocytes, or new postovulatory follicles in the ovary

*Spawned the night before capture*: postovulatory follicles 12 to 30 hours old in the ovary

*Spawned two nights before capture*: postovulatory follicles 36 to 54 hours old in the ovary.

Some histological stages were not used to estimate spawning frequency because we were not confident that their incidence could be consistently determined. We did not use oocytes in the early migratory-nucleus stage, because we were not confident of the time of day when females became fully recruited into this stage. We show the data, however (spawning night A, table 2). It is interesting that the migratory-nucleus stage was first detected at 2000 hours, about 24 hours before the batch would be expected to spawn. We also did not use postovulatory follicles considered to be older than 55 hours, because they can be confused with very late stages of β atresia.

The percentage of mature females spawning per day is estimated from daily spawning rates computed for three different spawning nights: spawning night B, determined on the basis of females with ovaries containing hydrated oocytes or postovulatory follicles, and spawning nights C and D, based on females with ovaries containing postovulatory follicles of different ages. The percentages of mature females spawning on nights B, C, and D were 20.1%, 23.5%, and 16.9% (table 2). The mean of the three estimates was 20.2%, indicating that the average female *T. symmetricus* spawned every 5 days during the 18-day sampling period.

The ovaries of 8% of the mature females contained histological evidence of two spawnings: that is, a single ovary contained postovulatory follicles of two different ages; or postovulatory follicles and hydrated or migratory-nucleus-stage oocytes; or some other combination. Because we knew the approximate age for each of these characters, we were able to calculate the interval between spawnings. The data indicated that 8% of the population spawned at intervals of one to three days (table 3).

### *Batch Fecundity*

The relation between female weight ($W$, without ovary) and batch fecundity ($F$) for 33 females with batch fecundity estimates (table 4) was determined by linear regression analysis. In the resulting equation, $F = -11436 + 126W$ with $r^2 = 0.48$, the intercept for the regression of $F$ on $W$ did not differ from zero ($t = -0.62$, df = 32, $P = 0.541$). Therefore, the regression line was forced through 0, yielding the relation $F = 112W$, where $W$ ranged from 586 to 1,262 g (figure 2).

Covariance analysis indicated that the relation between batch fecundity and female weight was different when the ovary contained postovulatory follicles >11 hours old ($F_{1,30}$ 20.94, $P < 0.001$), and the $r^2$ improved to 0.68 in the multiple regression equation with the presence of past spawning as a variable. Thus females that had spawned within the last 12–54 hours had lower batch fecundity than those in which no evidence of past spawning was detected. The mean adjusted fecundity for the average (791 g, without ovary) female in our fecundity data set was 73,655 oocytes (SE = 1,116) when evidence existed for past spawning, and 103,797 oocytes (SE = 1,181) when no such evidence existed.

*T. symmetricus* ovaries usually contained substantially more advanced yolked oocytes than are released in a single spawning batch. This is in sharp contrast to the northern anchovy, in which most of the advanced-yolked oocytes become hydrated and

TABLE 2
**Spawning Frequency of *T. symmetricus* on Four Nights (A–D) and the Presence of Histological Characters Indicating Spawning**

| | | Spawning nights | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | A | B | | | C | D | |
| Midpoint hour | Trawl ID number | Early migratory-nucleus-stage oocytes | Hydrated oocytes | Hydrated oocytes & new postovulatory follicles | Postovulatory follicles 0–6 hours old | Postovulatory follicles 12–30 hours old | Postovulatory follicles 36–54 hours old | Total number mature females |
| 1200 | 29 | 0 | 0 | 0 | 0 | 1 | 0 | 6 |
| 1400 | 8 | 0 | 4 | 9 | 0 | 4 | 2 | 21 |
| 1500 | 1 | 0 | 1 | 1 | 0 | 3 | 1 | 11 |
| 2000 | 17 | 2 | 0 | 2 | 5 | 7 | 2 | 19 |
| | 6 | 3 | 0 | 4 | 1 | 2 | 6 | 20 |
| | 22 | 1 | 0 | 2 | 3 | 9 | 2 | 20 |
| | 24 | 1 | 0 | 0 | 0 | 2 | 3 | 5 |
| | 2 | 4 | 0 | 0 | 2 | 1 | 1 | 20 |
| | 19 | 3 | 0 | 5 | 1 | 7 | 5 | 20 |
| 2100 | 13 | 1 | 1 | 2 | 0 | 7 | 4 | 21 |
| | 15 | 4 | 0 | 1 | 1 | 4 | 6 | 20 |
| | 32 | 5 | 0 | 0 | 0 | 2 | 2 | 18 |
| | 9 | 3 | 0 | 1 | 3 | 0 | 2 | 10 |
| | 34 | 3 | 0 | 1 | 1 | 2 | 1 | 20 |
| 2200 | 11 | 2 | 3 | 0 | 4 | 5 | 6 | 20 |
| | 28 | 5 | 0 | 0 | 1 | 4 | 5 | 21 |
| | 27 | 2 | 0 | 0 | 0 | 5 | 5 | 22 |
| 24/0 | 36 | 0 | 0 | 0 | 0 | 1 | 1 | 10 |
| | 7 | 3 | 0 | 0 | 4 | 4 | 5 | 20 |
| | 3 | 5 | 0 | 1 | 0 | 1 | 2 | 18 |
| | 18 | 4 | 1 | 0 | 7 | 7 | 3 | 21 |
| 0100 | 20 | 3 | 0 | 0 | 2 | 3 | 3 | 10 |
| 0200 | 31 | 0 | 0 | 0 | 0 | 0 | 0 | 5 |
| 0300 | 10 | 1 | 0 | 1 | 4 | 4 | 2 | 10 |
| | 23 | 1 | 0 | 0 | 1 | 4 | 0 | 5 |
| 0400 | 33 | 0 | 0 | 0 | 1 | 3 | 1 | 10 |
| 0600 | 26 | 3 | 0 | 0 | 2 | 5 | 0 | 10 |
| All | N | 59 | 10 | 30 | 43 | 97 | 70 | 413 |
| Females spawning per night | %<br>SE | 14.3<br>1.8 | | 20.1<br>3.5 | | 23.5<br>2.6 | 16.9<br>1.9 | |

Some females have more than one histological character, but no female is counted more than once per given spawning night.

are spawned as a single batch. In the 33 females used to estimate batch fecundity, we also measured the size and estimated the number of the remaining advanced-yolked oocytes (not included in the spawning batch). We determined that the ratio of the number of oocytes in the fecundity batch to the remaining advanced-yolked oocytes was 1.01 (SD = 0.41) and that the average mean diameter of the remaining advanced-yolked oocytes was 0.55 mm (SD = 0.026). Thus, just before spawning, there existed the equivalent of about two batches of advanced-yolked oocytes, one of which would definitely be spawned. Under some circumstances (such as higher water temperature, reduced food availability, or the last spawn) all the advanced oocytes may be hydrated and spawned at once, thus doubling the batch fecundity. Our results also indicated that size modes of oocytes, or an oocyte size threshold should not be used as an alternative to counts of oocytes in the hydrated or migratory-nucleus stages, because they may yield inaccurate estimates of batch fecundity in *T. symmetricus*.

To estimate how many batches of yolked oocytes an ovary contained, we counted all the oocytes larger than 0.25 mm in the ovaries of the three females (A, B, and C) illustrated in figure 3. Histological criteria indicate that 0.25 mm is about the diameter of an oocyte at the onset of vitellogenesis. By dividing the total number of oocytes larger than 0.25 mm by their batch fecundity, we obtained estimates of 6, 4, and 7 batches for females A–C, respectively. Thus *T. symmetricus* ovaries may contain

TABLE 3
**Occurrence (+) of Histological Criteria in the Ovaries of 33 Spawning *T. symmetricus* Females Indicating Different Spawning Events**

| Trawl # | Fish number[a] | Migratory-nucleus oocytes | Postovulatory follicles | | | Elapsed time between spawnings (day) |
|---|---|---|---|---|---|---|
| | | | ≤6 hours old[b] | 12–30 hours old | 36–54 hours old | |
| 11 | 1604 | – | + | + | – | 1 |
| 17 | 1633 | – | + | + | – | 1 |
| 3 | 1617 | + | – | + | – | 2 |
| 7 | 1610 | + | – | + | – | 2 |
| 17 | 1601 | + | – | + | – | 2 |
| 18 | 1608 | + | – | + | – | 2 |
| 18 | 1620 | + | – | + | – | 2 |
| 19 | 1647 | + | – | + | – | 2 |
| 19 | 1649 | + | – | + | – | 2 |
| 23 | 1628 | + | – | + | – | 2 |
| 26 | 1603 | + | – | + | – | 2 |
| 26 | 1605 | + | – | + | – | 2 |
| 26 | 1607 | + | – | + | – | 2 |
| 27 | 1613 | + | – | + | – | 2 |
| 28 | 1617 | + | – | + | – | 2 |
| 32 | 1618 | + | – | + | – | 2 |
| 8 | 1619 | – | + | – | + | 2 |
| 10 | 1607 | – | + | – | + | 2 |
| 18 | 1617 | – | + | – | + | 2 |
| 22 | 1611 | – | + | – | + | 2 |
| 6 | 1618 | + | – | – | + | 3 |
| 7 | 1605 | + | – | – | + | 3 |
| 9 | 1610 | + | – | – | + | 3 |
| 10 | 1604 | + | – | – | + | 3 |
| 11 | 1602 | + | – | – | + | 3 |
| 15 | 1612 | + | – | – | + | 3 |
| 17 | 1625 | + | – | – | + | 3 |
| 18 | 1628 | + | – | – | + | 3 |
| 19 | 1608 | + | – | – | + | 3 |
| 20 | 1618 | + | – | – | + | 3 |
| 24 | 1699 | + | – | – | + | 3 |
| 27 | 1620 | + | – | – | + | 3 |
| 28 | 1602 | + | – | – | + | 3 |

[a] Females are listed in order of time elapsed between spawnings.
[b] Ovary may also contain hydrated oocytes; ovaries of two females (11–1604 and 18–1617) contained only hydrated oocytes. Because spawning was imminent, they are included in this group.

the equivalent of 4–7 spawning batches of yolked oocytes, if one includes oocytes in the earliest vitellogenic stages.

### *Annual Spawning Cycle and Ovarian Atresia*

The atretic state of *T. symmetricus* ovaries taken in this study is best considered within the context of the annual spawning cycle. According to monthly averages of the standing stock of jack mackerel larvae in the California Current from 1951 to 1984 (Moser et al. 1993), about 27% of the season's production had been completed by the end of the cruise. During the cruise period, about 10% of the average number of larvae produced in a year were spawned (shaded area in figure 4).

Our analysis of ovarian atresia indicates that about 5% of the *T. symmetricus* in the collection area had ended or were close to ending spawning for the year. The ovaries of 3 (0.7%) of the 413 mature females were classified as inactive and were judged not able to spawn at the time of capture or in the near future because they contained beta atresia but no yolked oocytes. The presence of beta atresia in these ovaries indicated that the ovaries may have been active during the current season (Hunter and Macewicz 1985b). An additional sign of season completion, for 4% of the females, was the presence in their ovaries of the alpha stage of atresia in 50% or more of the yolked oocytes (Hunter and Macewicz 1980, 1985b). This lends credence to our assumption that this highly atretic condition is related to the end of spawning for female *T. symmetricus*. Finally, the small loss (4.7%) of females to the spawning population seems reasonable, since only about a fourth of the production for the spawning season had been completed.

TABLE 4

**Batch Fecundity (Number of Oocytes to Be Spawned in the Batch) of 33 *T. symmetricus* Females Taken March 23–April 9, 1991, and 2 Females Taken May 27, 1970**

| Year | Fork length (mm) | Weight without ovary (g) | Ovary weight (g) | Batch fecundity | Postovulatory follicles* |
|---|---|---|---|---|---|
| 1991 | | | | | |
| | 383 | 586.4 | 24.612 | 51,987 | + |
| | 393 | 598.2 | 44.786 | 52,965 | + |
| | 395 | 605.5 | 21.508 | 52,147 | – |
| | 415 | 632.9 | 31.102 | 63,997 | + |
| | 398 | 637.7 | 26.343 | 52,736 | + |
| | 382 | 638.5 | 47.462 | 75,915 | – |
| | 396 | 643.8 | 41.250 | 56,395 | – |
| | 400 | 654.6 | 62.410 | 82,476 | + |
| | 394 | 659.3 | 31.707 | 73,392 | + |
| | 406 | 665.0 | 47.000 | 109,593 | – |
| | 412 | 668.8 | 25.230 | 61,628 | + |
| | 403 | 671.4 | 22.568 | 31,752 | + |
| | 406 | 697.6 | 29.357 | 72,269 | – |
| | 417 | 706.2 | 27.754 | 86,400 | – |
| | 413 | 722.5 | 25.455 | 48,360 | + |
| | 405 | 735.8 | 33.952 | 70,205 | + |
| | 423 | 739.9 | 32.126 | 59,946 | + |
| | 422 | 744.8 | 29.226 | 91,661 | – |
| | 429 | 755.5 | 42.482 | 129,838 | – |
| | 417 | 756.7 | 35.283 | 100,267 | – |
| | 423 | 761.7 | 99.310 | 115,847 | – |
| | 422 | 775.4 | 32.637 | 81,073 | + |
| | 432 | 776.7 | 40.255 | 123,961 | – |
| | 421 | 793.5 | 35.530 | 85,795 | – |
| | 435 | 826.8 | 54.153 | 120,063 | – |
| | 454 | 902.3 | 39.669 | 72,685 | + |
| | 445 | 904.3 | 64.735 | 112,648 | – |
| | 440 | 945.8 | 63.191 | 134,716 | – |
| | 485 | 1105.9 | 46.083 | 94,654 | + |
| | 493 | 1160.8 | 64.237 | 164,711 | + |
| | 492 | 1162.8 | 58.214 | 116,788 | + |
| | 504 | 1194.3 | 58.669 | 94,543 | + |
| | 488 | 1262.4 | 123.550 | 171,466 | – |
| 1970 | | | | | |
| | 543 | 1576.2 | 141.8 | 192,000 | * |
| | 540 | 1602.0 | 120.0 | 159,000 | * |

*+ = presence of postovulatory follicles 12 to 54 hours old, indicating these females had spawned recently.
* = unknown if postovulatory follicles were present, data are from MacGregor 1976.

About a third of the females had ovaries containing minor levels of alpha-stage atresia (less than 50% of yolked oocytes affected). This condition seemed surprisingly common (35% of the mature females), since only a fourth of the season's production had been completed. In comparison, during the peak months of the northern anchovy spawning season, females classed in this state—i.e., containing minor levels of alpha atresia—constitute only about a twentieth of the population (Hunter and Macewicz 1985b).

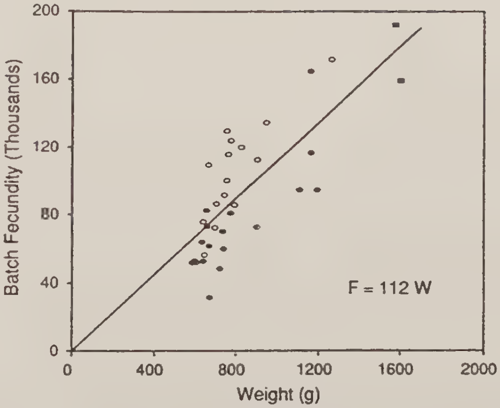

Figure 2. Batch fecundity (F) of *Trachurus symmetricus* as a function of female weight (W, without the ovary); the batch was estimated from numbers of migratory-nucleus-stage oocytes or hydrated oocytes; regression line was forced through zero. *Closed circles* = females that had spawned 12 to 54 hours before capture; *open circles* = females with no histological evidence of a past spawning; *Squares* = females with unknown spawning history, from MacGregor 1976.

## DISCUSSION

This study indicates that jack mackerel, *Trachurus symmetricus*, females spawn many times during the year. The average *T. symmetricus* female spawned 3.6 times during the 18-day sampling period. Over the same period about 10% of the annual crop of *T. symmetricus* larvae were produced (figure 4), according to the annual larval production curve from Moser et al. (1993). Thus the average female may spawn 36 times per year according to these data.

Data from two other studies indicate high spawning rates in *T. symmetricus*. The frequency of *T. symmetricus* females with ovaries containing hydrated oocytes ranged from 0 to 24% in monthly sets of samples compiled over several years by Wine and Knaggs (1975) from southern California data. Wine and Knaggs did not intend for their data to be used to estimate spawning frequency, and biases could exist because of sampling during inappropriate times of day (DeMartini and Fountain 1981; Schaefer 1987). Lisovenko and Andrianov (1991) used the hydrated-oocyte method to estimate spawning frequency for *Trachurus murphyi* taken off Peru in 1980–85. Our interpretation of their data indicate that the average *T. murphyi* female may spawn about 15 times per year. Wine and Knaggs's data indicate about 21 spawnings for *T. symmetricus*, whereas our initial guess for *T. symmetricus*, based on our point estimate and the average larval production curve, was about 36 spawnings. All data considered, 25 spawnings per year seems a reasonable guess of the annual number of spawnings for the average female *Trachurus*. This means that the average *T. symmetricus* female may spawn about 2,800 oocytes per gram

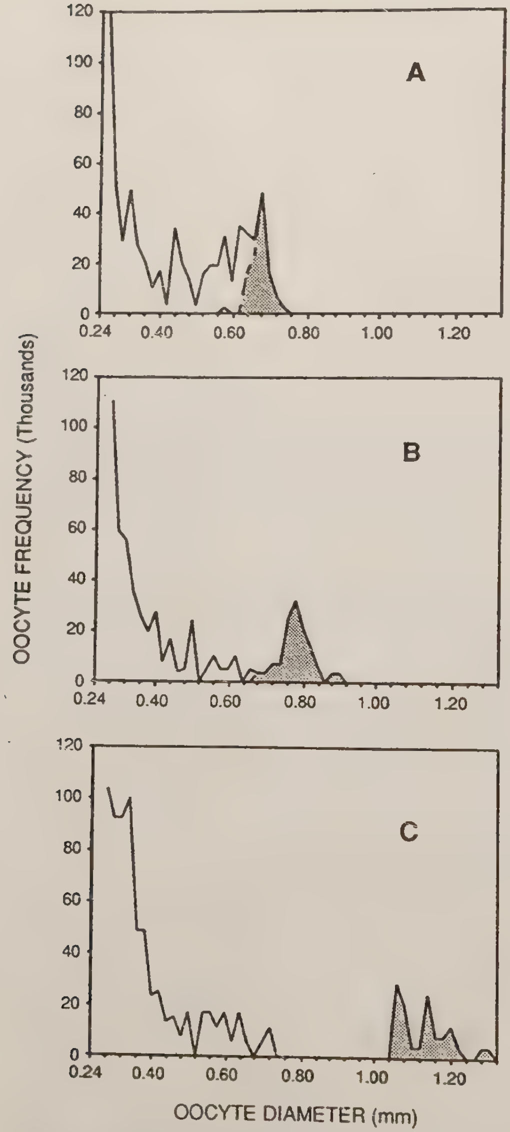

Figure 3. Oocyte size-frequency distributions of three *Trachurus symmetricus* females showing progressive maturation of a spawning batch from female A to female C. *Shaded area* = batches about to be spawned: in *A*, early migratory-nucleus-stage oocytes (mean diameter = 0.67 mm); in *B*, well-advanced migratory-nucleus-stage oocytes (mean diameter = 0.78 mm); and in *C*, hydrated oocytes (mean diameter = 1.13 mm).

body weight per year (25 × 112). More accurate data, particularly age-specific data, would be highly desirable.

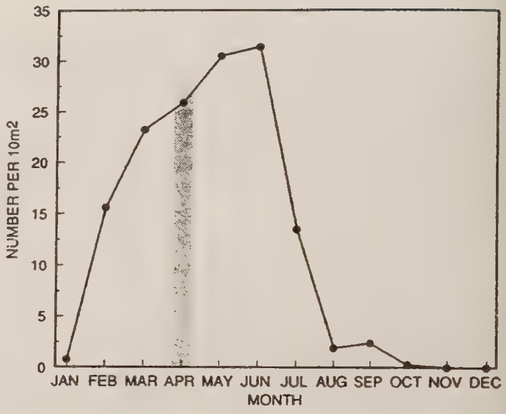

Figure 4. Annual spawning season as indicated by the average number of *Trachurus symmetricus* larvae per 10 m² taken in the CalCOFI surveys 1958–84, from Moser et al. 1993. *Shaded area* indicates portion of spawning season considered in this paper.

The potential annual fecundity of various *Trachurus* species has been estimated over the years (Chigirinskiy 1970; Kaiser 1973; Macer 1974; Andrianov 1985; Arruda 1986), but we suspect these data are a loss. Owing to the high spawning rates of *Trachurus* indicated by this study and the two cited above, and the limited number of batches of yolked oocytes in the ovary, it seems unlikely that the standing stock of yolked oocytes in the ovary at the beginning of the spawning season is an accurate measure of annual fecundity in any *Trachurus* species. In other words, it is probably preferable to consider annual fecundity as being indeterminate in *Trachurus*. Thus the only accurate way to measure annual fecundity is to measure spawning frequency and batch fecundity throughout the spawning season.

Only a few studies of batch fecundity exist for *Trachurus*, and most of these are not particularly useful for making comparisons. We believe that only the two determinations based on hydrated oocytes are useful in MacGregor's (1976) preliminary study of *T. symmetricus*; for the other 28 of his specimens, MacGregor may have used inaccurate criteria (all dense-yolked oocytes) to identify the oocytes composing the batch in *T. symmetricus*. Paschenko[1] identified the spawning batch as all oocytes above 0.50 mm (as shown in MacGregor 1976, figure 2) so his fecundities are probably overestimated. It is obvious from our few oocyte size-frequency distributions that all the dense-yolked oocytes are not spawned at once, because only about half of them undergo final maturation synchronously. Chigirinskiy (1970) also used an inaccurate oocyte criterion for identifying the spawning batch of *T. japonicus* (yolked oocytes >0.38-mm diameter). Although Lisovenko and Andrianov (1991) used hydrated oocytes to identify the oocytes composing the spawning batch in *T. murphyi*, they do not give the weight or length of the females; consequently, comparison to their study is difficult. The most useful study is that of Dioses et al. (1989), who used hydrated oocytes to estimate batch fecundity of *T. murphyi* off Peru. The relative batch fecundity of *T. murphyi* in his study—about 235 oocytes per gram female weight—is about twice that of *T. symmetricus* in this study (112 oocytes per gram).

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[1] Paschenko, V. M. Distribution, biology and biomass assessment of the jack mackerel *Trachurus symmetricus* (Ayres). Presented to the 1979 U.S.–U.S.S.R. Bilateral Meeting on Fisheries Assessment in the North Pacific, Seattle, June 5–8, 1979.

Batch fecundity may change seasonally in *T. symmetricus*, as it does in a number of other fishes (Conover 1985; Alheit 1987; Kjesbu 1989). Two kinds of indirect evidence suggest a possible seasonal change in batch fecundity. First, females with low levels of ovarian atresia were more prevalent than expected, considering that only 27% of the year's spawnings had been completed. These females appeared to continue spawning at undiminished rates, but atretic losses may have reduced the batch size. Second, batch fecundity was lower in females with evidence of past spawning, indicating that there may be a link between batch fecundity and spawning rate.

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# Lipid Dynamics in Relation to the Annual Reproductive Cycle in Yellowtail Rockfish (*Sebastes flavidus*)

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MacFarlane, R. B., E. C. Norton, and M. J. Bowers. 1993. Lipid dynamics in relation to the annual reproductive cycle in yellowtail rockfish (*Sebastes flavidus*). Can. J. Fish. Aquat. Sci. 50: 391–401.

In yellowtail rockfish (*Sebastes flavidus*), lipids that accumulated in mesenteries and liver during the summer and early fall upwelling were subsequently translocated to developing ovaries during late fall and winter. Tissue and serum lipids were assessed by stage of ovary maturation from fish collected monthly over six annual reproductive cycles (1985–91) from Cordell Bank, a seamount off central California. Lipids were primarily transported to ovaries prior to fertilization. Energetic lipids (triglycerides, nonesterified fatty acids) were maximal in serum during yolk accumulation stages and declined significantly during embryonic stages. Between fertilization and parturition, lipid and protein content of ovaries declined by about 21%, a value approaching the minimum for lecithotrophy (i.e. ovoviviparity). During gestation, however, serum phospholipids and calcium (vitellogenin surrogate) were significantly elevated relative to male levels, suggesting matrotrophic contributions. A reproductive mode that is primarily lecithotrophic but supplemented by maternal inputs during embryogenesis would be beneficial to viviparous fishes of the California coast. This strategy may optimize reproduction by coupling the disparate times of food abundance and gestation, yet allow for provision of nutrients late in the reproductive cycle should they be available.

Chez le sébaste à queue jaune (*Sebastes flavidus*), les lipides qui se sont accumulés dans le mésentère et le foie au cours de l'été et lors de l'upwelling tôt en automne, ont par la suite été transportés jusqu'aux ovaires en développement au cours de la fin de l'automne et en hiver. Les lipides contenus dans les tissus et le sérum ont été dosés en fonction des étapes de maturation de l'ovaire chez des poissons prélevés chaque mois pendant six cycles reproductifs annuels (1985–1991) et qui provenaient de Cordell Bank, un mont sous-marin situé au large de la partie centrale de la Californie. Les lipides ont d'abord été transportés jusqu'aux ovaires avant la fécondation. La concentration en lipides calorigènes (triglycérides, acides gras non estérifiés) était maximale dans le sérum au cours des étapes d'accumulation du vitellus et diminuait sensiblement au cours des stades embryonnaires. Entre la fécondation et la ponte, la teneur en lipides et en protéines des ovaires a diminué d'environ 21 %; cette valeur confine au minimum requis pour définir la lécithotrophie (c.-à-d. ovoviviparité). Cependant, pendant la maturation des oeufs dans l'organisme, la concentration en calcium et en phospholipides sériques (substitut de la vitellogénine) a été significativement élevée par rapport à la teneur observée chez les mâles, ce qui nous amène à envisager des contributions caractéristiques du système reproducteur de la femelle. Un mode de reproduction qui est avant tout lécithotrophe, mais qui est complété par des apports maternels durant l'embryogenèse présenterait un avantage pour les poissons vivipares de la côte de la reproduction en permettant de faire le pont entre des époques différentes d'abondance des aliments et d'embryogenèse, mais en assurant la disponibilité d'éléments nutritifs tard dans le cycle de la reproduction.

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The coastal region of California is subject to variable seasonal upwelling (Boje and Tomczak 1978). Upwelling onset, duration, and intensity, and perhaps advection by the California Current (Bernal and McGowan 1981), modulate the trophodynamics of coastal fish communities (Hobson and Chess 1988). The nutritional state of many fish species within this system is tied to the temporal pattern of productivity produced by these influences.

Rockfish (*Sebastes*) are dominant components of fish communities within the California upwelling region. These viviparous species respond to changes in environmental conditions by annually and interannually varying the accumulation of lipids. Lipid accumulation may influence reproduction (Larson 1991), but Guillemot et al. (1985) interpreted seasonal (i.e. quarterly) changes in mesenteric fat volume in four species of rockfish as having little or no reproductive function. They conjectured that since there was overlap in fat and gonad cycles, lipid reserves acquired in the summer and fall were used primarily for adult maintenance functions during the winter. Yet, yellowtail rockfish (*Sebastes flavidus*), one of the species assessed by Guillemot et al. (1985), had impaired reproduction that corresponded to low fat deposits during the 1983 El Niño (Lenarz and Wyllie Echeverria 1986).

In marine fishes, lipids are the major source of nutrition (Sargent 1976; Sargent et al. 1989). When maternal diets are deficient, insufficient transfer of lipids to developing ovaries may reduce fecundity and the viability of the progeny (Watanabe 1985; Luquet and Watanabe 1986; Heming and Buddington 1988). Indeed, fluctuations in the quantity and/or quality of larvae released due to variations in food availability are potential contributors to the significant interannual variability of recruitment strength found in rockfish (Moser and Boehlert 1991).

Despite the apparent importance of lipids to ovarian development, data exist primarily for oviparous teleosts. Information is limited temporally, or by lipid components and tissues assayed (Luquet and Watanabe 1986; Kjorsvik et al. 1990). Even less information is available for viviparous teleosts (e.g. see Pekkarinen and Kristoffersson 1975; Korsgaard and Petersen 1979). For species of the genus *Sebastes*, nothing is known of lipid dynamics beyond mesenteric fat variations.

Since April 1985, we have studied the reproductive biology of a population of *S. flavidus* living on Cordell Bank, a seamount off the central coast of California. This paper presents the results of our investigation of lipid dynamics in yellowtail rockfish during the annual reproductive cycle. Lipids in serum, gonad, liver, mesenteries, and muscle tissues were evaluated temporally and by stage of ovarian maturation to elucidate the relationship of lipid components to specific oocyte and embryonic developmental stages.

## Materials and Methods

Adult yellowtail rockfish were obtained by hook and line at depths ranging from 50 to 150 m from Cordell Bank, a seamount 37 km west of Pt. Reyes, California. Specimens were collected monthly from April 1985 through March 1991, except for June 1985 and November 1986 (rough sea conditions) and several months between May 1988 and November 1989 (operational research constraints). Approximately 10 females and 5 males were examined monthly from May 1987 to the end of the study; prior to May 1987, only females were assessed.

Immediately after capture, blood was obtained by cardiac puncture using sterile Vacutainers without anticoagulant and allowed to clot before centrifugation for serum isolation. Fish were held on ice until examination, dissection, and tissue subsampling were performed (within 24 h). Following morphometric determinations, liver, gonad, and muscle samples were frozen at −70°C for later lipid analysis. Ovary sections were excised and fixed in 10% neutral buffered formalin for histological preparation. Paraffin-embedded, hematoxylin-, and eosin-stained sections of oocytes and embryos were categorized into one of nine stages of development according to the following ovary maturation stage (OMS) classification scheme (Bowers 1992):

| OMS | State of development |
|---|---|
| 1 | Recovery (early recrudescence) |
| 2 | Early yolk accumulation |
| 3 | Late yolk accumulation |
| 4 | Migratory nucleus |
| 5 | Ovulation and fertilization |
| 6 | Early-celled embryo |
| 7 | Embryonic body |
| 8 | Eyed larvae |
| 9 | Spent |

We recorded each specimen's sex, standard length, and total weight and the weights of liver, gonad, and mesenteric fat. We calculated each tissue's relative weight index (i.e. liver somatic (LSI), gonadosomatic (GSI), and mesenteric fat index (MFI), respectively) as (tissue weight/body weight) × 100. The age of each fish was determined by counting annual growth increments of otoliths using routine break-and-burn techniques.

Serum triacylglycerols (triglycerides), total cholesterol, and calcium were measured by a computerized Technicon sequential multiple analyzer (SMAC) according to the procedures supplied by the manufacturer (Technicon Instruments Corp., Tarrytown, NY). Serum calcium concentrations were used as an indicator of serum vitellogenin (Tinsley 1985). Calcium is stoichiometrically incorporated into vitellogenin and correlates with ovarian but not testicular maturation (Ng and Idler 1983; Mommsen and Walsh 1988). References to vitellogenin in this paper are based on serum calcium determinations. Serum phospholipids and nonesterified fatty acids were quantified by in vitro enzymatic colorimetric methods using test kits purchased from Wako Pure Chemical Industries, Ltd., Osaka, Japan.

Total lipids were extracted in duplicate from 1–2 g of liver, gonad, and muscle tissues by the biphasic method of Bligh and Dyer (1959) following homogenization using a Polytron (Brinkmann Instruments Co., Westbury, NY). After December 1988, a different extraction technique was used. Frozen tissue samples were minced into thin 2-mm slices and extracted in sufficient chloroform–methanol (2:1, v/v) to achieve a final concentration of about 30 μg/μL. Lipids were extracted for 24 h with occasional stirring; subsequently, an additional 5.0 mL of solvent was added and extraction continued for another 24 h. Triplicate determinations of three separate livers revealed no significant differences in mean lipid concentrations between the two extraction techniques (ANOVA, $P = 0.31$).

Total lipids were quantified by thin layer chromatography combined with flame ionization detection (TLC-FID) using an Iatroscan TH-10 Mark III (Iatron Laboratories Inc., Tokyo, Japan) interfaced with T Datascan software (RSS Inc., Costa Mesa, CA). Triplicate 1.0-μL aliquots were spotted on Chromarods S-III, dried, and scanned at 3.1 mm/s, hydrogen pressure of 0.95 kg/cm$^2$, and air flow of 2000 mL/min. Chromarods were stored desiccated, cleaned with 9 N $H_2SO_4$, rinsed with Milli-Q water, and activated by two passes through the FID. Peak areas were converted to lipid weight by comparison with external standard curves created from dilutions of gravimetrically measured lipid extracts from *S. flavidus* livers.

Ovary protein concentrations were analyzed by the Lowry method using bovine serum albumin standards (Lowry et al. 1951).

Temporal variations of lipids and lipid concentration relationships to stage of ovarian maturation were analyzed by general linear model (GLM) ANOVA procedures within SAS computer software (SAS Institute Inc., Cary, NC). If age or length was related to a variable's value, this effect was removed using the ANCOVA option in the GLM procedure. Comparisons between means were accomplished by Tukey's Studentized range (HSD) test, which controls the maximum experimentwise error rate, and paired *t*-tests.

To assess the change in weights of ovary lipid and protein according to OMS, these variables were adjusted for differences in female size by ANCOVA within the GLM procedure in SAS. The natural logarithm of standard length was used as the covariate, since it stabilizes the variance among means and approximates the relationship between body weight and length. Total body weight varies in relation to length due to increasing ovary weight during reproductive development. Therefore, it cannot be used as a covariate to improve the precision of determining the relationship between tissue component quantity and OMS independent of fish size.

## Results

### Temporal Variations

Fluctuations of lipids during the annual reproductive cycle were evaluated on specimens collected monthly between May 1987 and April 1988 (Table 1). This interval covered one reproductive cycle starting from the onset of ovarian

TABLE 1. Mean (±SE) standard lengths and ages of *S. flavidus* assessed during the reproductive cycle in 1987–88. Means among months within the same sex are significantly different: $^{*}P < 0.05$; $^{**}P < 0.001$.

| Month | Females | | | Males | | |
|---|---|---|---|---|---|---|
| | Standard length (cm) | Age (yr) | $n$ | Standard length (cm) | Age (yr) | $n$ |
| May | 33.0 ± 0.1 | 8 ± 1 | 6 | 37.2 ± 0.6 | 26 ± 6 | 4 |
| June | 37.2 ± 1.4 | 16 ± 3 | 8 | 35.1 ± 0.7 | 13 ± 2 | 7 |
| July | 41.2 ± 0.9 | 20± 2 | 11 | 37.4 ± 1.7 | 15 ± 3 | 4 |
| August | 38.3 ± 0.8 | 18 ± 2 | 10 | 35.0 ± 0.8 | 17 ± 3 | 5 |
| September | 35.5 ± 1.2 | 13 ± 3 | 10 | 32.0 | 8 | 1 |
| October | 37.9 ± 1.0 | 18 ± 2 | 10 | 34.6 ± 0.8 | 14 ± 3 | 5 |
| November | 37.6 ± 1.1 | 18 ± 2 | 10 | 37.1 ± 0.9 | 17 ± 3 | 4 |
| December | 36.6 ± 1.1 | 16 ± 2 | 10 | 34.7 ± 1.0 | 19± 3 | 5 |
| January | 37.0 ± 1.9 | 14 ± 3 | 7 | 35.7 ± 0.6 | 16 ± 2 | 6 |
| February | 32.5 ± 1.2 | 11 ± 2 | 8 | 33.3 ± 0.6 | 15 ± 2 | 7 |
| March | 38.2 ± 1.0 | 20± 3 | 10 | 34.5 ± 1.5 | 17 ± 5 | 5 |
| April | 36.8 ± 1.4 | 14 ± 2 | 8 | 36.0 ± 0.8 | 22 ±5 | 5 |
| Total | 37.0 ± 0.4** | 16 ± 1* | 108 | 35.3 ± 0.3* | 17 ± 1 | 58 |

recrudescence in May and terminating with parturition of larvae in February and March. Data from fish collected in April reveal the start of the next cycle. Since the male reproductive cycle precedes that of the female, data from males were used to assess changes in females specific to the cycle of ovarian development. Significant differences among monthly mean length or age were not important for analysis of lipid variables during the 12 mo assessed. Only GSI and MFI varied significantly with length; no variables were affected by age differences.

The gonadal cycles of females and males are not synchronous in *S. flavidus* (Fig. 1). Maximum testicular size was in August when copulation occurred whereas ovaries did not enlarge until November. Histologically, initial yolk accumulation become apparent in July and persisted for at least 6 mo.

Mesenteric fat and liver mass increased significantly ($P < 0.0001$) until August and remained elevated through November in females (Fig. 1). Whereas liver mass increased evenly in both sexes, females gained greater amounts of fat in their intestinal mesenteries than males from August through November ($P < 0.05$). As ovaries matured through fertilization, embryogenesis, and parturition, liver mass and mesenteric fat declined. These somatic trends also occurred in males during this interval.

Serum levels of triglycerides, nonesterified fatty acids (NEFA), and phospholipids were similar in females and males during the summer and early fall months except for September (Fig. 2). The mean triglyceride level in female serum in September (1979 ± 152 mg/dL) was more than twice the highest level recorded during the 6 yr of the study and should be considered anomalous. This was also true for NEFA in females. Serum cholesterol levels were indistinguishable between the sexes for the entire reproductive cycle except in August ($P < 0.05$).

During the winter months spanning late yolk accumulation and embryonic stages, serum lipids (except cholesterol) in females were significantly elevated over those in males ($P < 0.05$) (Fig. 2). In October, serum calcium levels in females (indicative of vitellogenin transport) became increasingly greater than in males ($P < 0.05$), attained maximal differences in December ($P < 0.0001$), and returned to the same levels in March, following parturition (Fig. 2).

Total lipid concentrations in liver were similar throughout the year in females and males (Fig. 3). Liver lipid fluctuated considerably during the reproductive cycle. In females, maximal concentrations occurred in August and declined to minimal values during January–March when parturition was completed.

During the annual cycle, lipid concentrations were elevated in ovaries from October through February($P < 0.001$), concurrent with increased ovary size (Fig. 3). Although concentrations of lipids in ovaries in April and in testes in June and January were high, the quantities were very low due to small gonad sizes. Testes lipids were below detection (5 μg) in February and March.

Muscle tissue contained relatively low concentrations of lipids in *S. flavidus* during the year (Fig. 3). Profiles of lipid concentration in muscle revealed no significant differences between the sexes throughout the reproductive cycle. There was little variation in lipid concentration of muscle between months.

### Variation in Maturation Stage

Although ovarian development is synchronous within a female, a range of OMS may exist at one time within the *S. flavidus* population. This is particularly the case during embryonic stages, since gestation lasts only about 30 d. Consequently, analyses by month do not reveal lipid levels during each OMS precisely. Therefore, changes in lipid concentrations by OMS were analyzed for the entire data set (April 1985 – March 1991). The mean length and age of fish analyzed for each OMS are presented in Table 2.

There was an inverse relationship between liver or mesenteric fat tissue amounts and the size of ovaries (Fig. 4). Liver and mesenteric fat increased significantly ($P < 0.05$) during early yolk accumulation (OMS 2) and declined ($P < 0.05$) during later oocyte and embryonic stages. Ovaries attained their largest size at the most advanced embryo stage, eyed larvae (OMS 8), when liver and mesenteric fat were minimal.

Serum lipid concentrations, as well as vitellogenin (measured as $Ca^{2+}$), in adult females were significantly different among OMS ($P < 0.0001$ for all variables) (Fig. 5). Triglycerides were greater in maternal serum during oocyte stages than during embryonic stages ($P < 0.05$). The NEFA were more

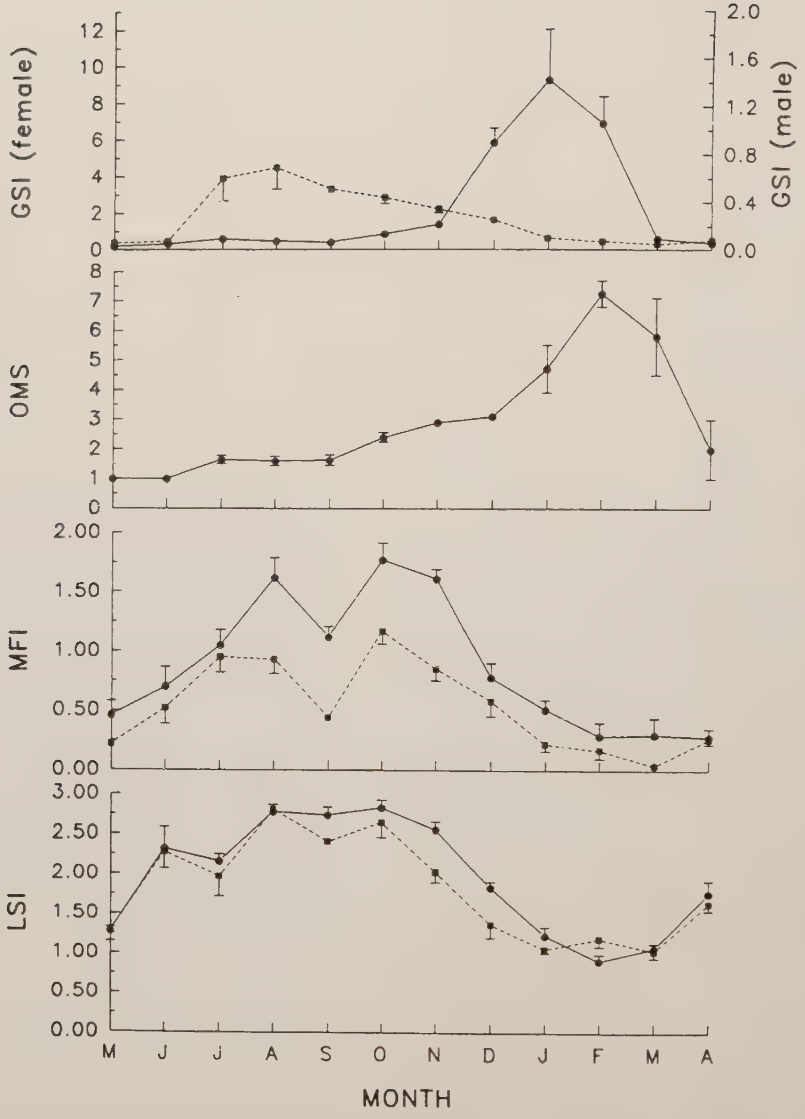

FIG. 1. Monthly variation of relative GSI, OMS, MFI, and LSI in *S. flavidus* for one reproductive cycle, May 1987 – April 1988. Values are means ± SE. Solid line, females; broken line, males.

variable than triglycerides but declined during embryonic stages as well ($P < 0.05$).

Cholesterol and phospholipids, which function predominantly as structural components, had somewhat different profiles in maternal serum relative to OMS than triglycerides or NEFA. Both lipid classes were significantly elevated ($P < 0.05$) during early-celled and embryonic body stages (OMS 6 and 7) compared with values during ovulation/fertilization (OMS 5) and eyed larvae (OMS 8) stages.

Serum calcium concentrations were statistically similar during OMS 3–8 but greater than during OMS 1, 2, and 9 ($P < 0.05$).

Tissue lipids were analyzed in fewer females (liver and ovary, $n = 284$; muscle, $n = 67$) than were analyzed for serum lipids and were randomly chosen from monthly collections (Fig. 6). Liver lipid, greatest in OMS 2, decreased significantly during gestation ($P < 0.05$). Lipid levels in muscle were low and not significantly different among OMS ($P = 0.20$). The greatest increases in lipid concentrations in ovaries occurred during OMS 3 and 4 (late yolk accumulation and migratory nucleus). Ovary lipids declined during gestational stages (OMS 5–8; $P < 0.05$).

The quantities of lipid and protein in ovaries attained maxima at the start of embryogenesis and experienced net declines

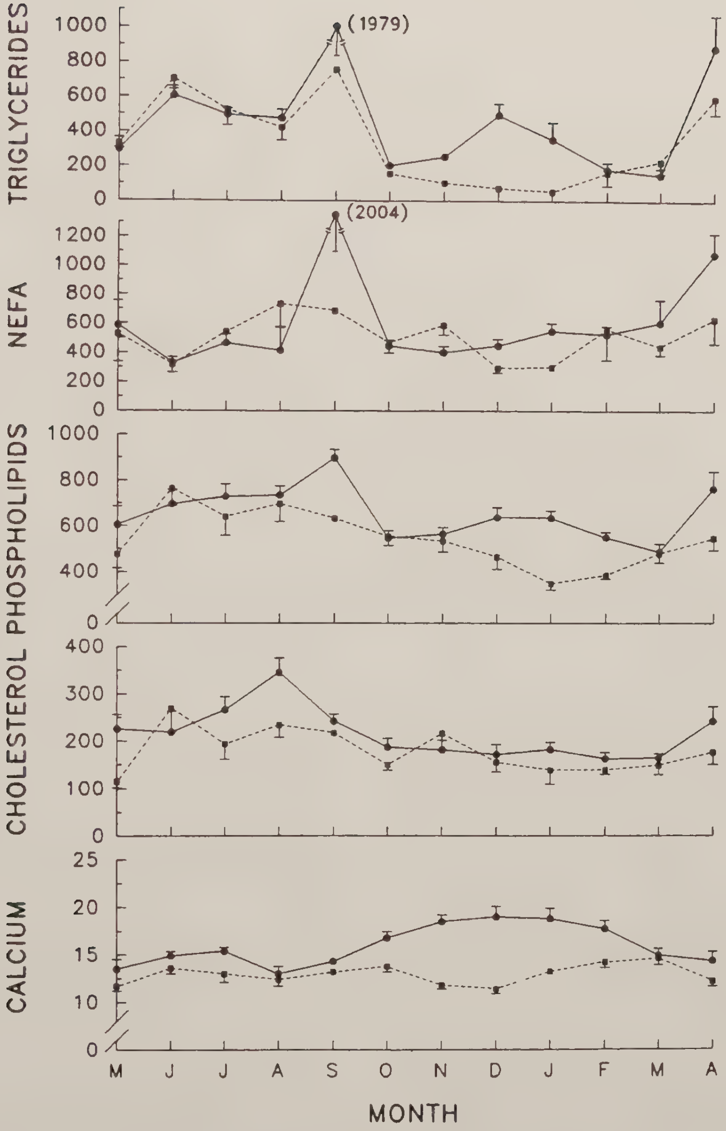

FIG. 2. Changes in serum triglycerides, NEFA, phospholipids, cholesterol, and calcium (vitellogenin surrogate) in *S. flavidus* during one reproductive cycle. Values are means ± SE in mg/dL except NEFA (μEq/L). Solid line, females; broken line, males.

through gestation (Fig. 7a). When lipid and protein quantities were converted to energy values, using factors of 39.6 and 20.1 kJ/g, respectively (Brett and Groves 1979), it became evident that maximum energy was sequestered in ovaries during OMS 6 (early-celled) or the start of embryogenesis (Fig. 7b). Greater energy was in the form of lipid during embryonic development whereas protein dominated quantitatively. Since OMS 5 (ovulation/fertilization) is an event rather than a developmental interval, and occurs during a very short time span, only three females' ovaries were assayed in this stage; therefore, the decline in lipid apparent in Fig. 7 is probably unrepresentative of that portion of the reproductive sequence.

## Discussion

Female yellowtail rockfish accumulate greater quantities of lipids in mesenteric depots than males during the active feeding period of summer and fall. Presumably this is advantageous to the maternal role in viviparity during the winter when food is

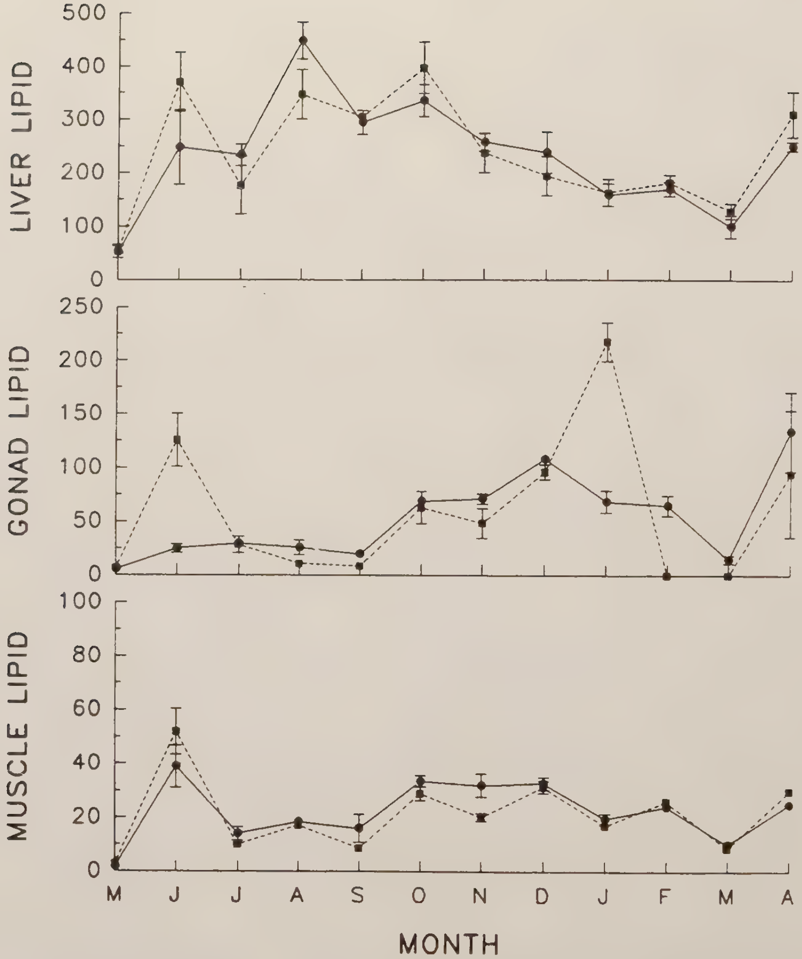

FIG. 3. Monthly concentration of total lipid in liver, gonad, and muscle of *S. flavidus* during one reproductive cycle. Values are means ± SE in mg/g fresh weight. Solid line, females; broken line, males.

TABLE 2. Mean (±SE) standard lengths and ages of female *S. flavidus* assessed by OMS. Females collected from April 1985 to March 1991. Means among stages are significantly different: $^{**}P < 0.001$.

| OMS | Description | Standard length (cm) | Age (yr) | *n* |
|---|---|---|---|---|
| 1 | Recovery | 37.2 ± 0.3 | 16 ± 1 | 166 |
| 2 | Early yolk | 38.5 ± 0.3 | 17 ± 1 | 94 |
| 3 | Late yolk | 38.4 ± 0.3 | 18 ± 1 | 156 |
| 4 | Migratory nucleus | 36.8 ± 0.6 | 16 ± 1 | 42 |
| 5 | Ovulation/fertilization | 33.3 ± 0.7 | 11 ± 2 | 3 |
| 6 | Early-celled embryo | 34.7 ± 0.8 | 13 ± 2 | 12 |
| 7 | Embryonic body | 37.0 ± 0.9 | 19 ± 2 | 30 |
| 8 | Eyed larvae | 36.1 ± 1.4 | 15 ± 2 | 12 |
| 9 | Spent | 36.5 ± 0.6 | 17 ± 1 | 48 |
| Total | | 37.5 ± 0.2** | 17 ± 1 | 563 |

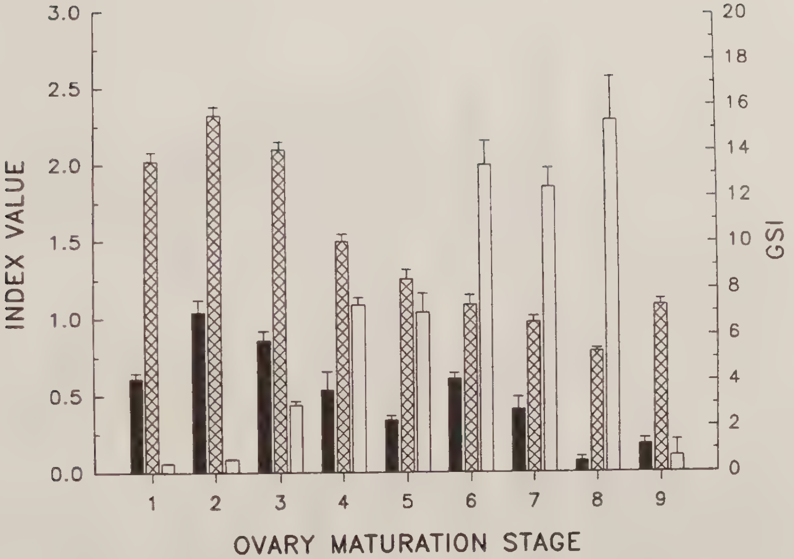

FIG. 4. Mean (+SE) values of LSI, MFI, and GSI by OMS of adult female *S. flavidus* from Cordell Bank, CA, collected between April 1985 and April 1991 (six reproductive cycles). MFI (solid bars) and LSI (cross-hatched bars) on left ordinate; GSI (open bars) on right ordinate. OMS: 1, recovering; 2, early yolk; 3, late yolk; 4, migratory nucleus; 5, ovulation/fertilization; 6, early-celled embryo; 7, embryonic body; 8, eyed larvae; 9, spent.

typically scarce on the central California coast (Bolin and Abbott 1963; Brinton 1976; Hobson and Chess 1988).

Lipids declined in mesenteries and liver as oocytes progressed from yolk accumulation through embryogenesis. During these stages, elevated lipid concentrations in maternal serum, relative to those of males, indicate that at least part of this transport was for female reproductive-specific purposes. Due to the increased body size of pregnant females, some of the mobilized triglycerides may be required for increased energy demands of functions such as locomotion and ion regulation, but the data suggest that a substantial portion was incorporated into developing ovaries. It is doubtful that energy costs of locomotion are high. Yellowtail rockfish are largely quiescent and do not migrate to any great extent (Carlson and Haight 1972; Carlson and Barr 1977). Further, serum glucose is quite low in *S. flavidus* (14.2 ± 0.5 mg/dL, $n = 487$), indicative of an inactive lifestyle (Love 1980).

Guillemot et al. (1985) measured changes in mesenteric fat volume across the annual reproductive cycle for several species of *Sebastes*, including *S. flavidus*. They described a pattern of fat accumulation similar to our results, but interpreted the data differently. They concluded that fat accumulation coincided with gametogenesis, and thus served primarily adult maintenance functions. Such a conclusion may have resulted from pooling data from several locations into yearly quarters. Our results, using monthly measurements and analysis by stage of ovarian maturation, clearly show an inverse relationship between liver and mesenteric fat quantity and ovarian development. Our data indicate that lipid stores acquired during the feeding period are destined for energy-requiring functions and structural proliferation in ovaries as well as for maintenance expenses of the adult during the poor feeding conditions of winter.

Viviparity in fishes can range from strict lecithotrophy, where embryonic nutrition is provided exclusively by energy reserves deposited during oogenesis, to extreme matrotrophy, where maternally contributed nutrients are provided only during gestation (Wourms 1981). Historically, members of the genus *Sebastes* have been considered lecithotrophic (Wourms 1991); however, recent evidence has suggested that this may not be the case for all rockfish species. Energy balance estimates (Boehlert and Yoklavich 1984; Boehlert et al. 1986; Dygert and Gunderson 1991) and in vitro incorporation of labeled glycine by embryos (Yoklavich and Boehlert 1991) indicated possible matrotrophy in several rockfish species.

Using conventional criteria to discriminate between lecithotrophic and matrotrophic viviparity, *S. flavidus* appear to be on the more lecithotrophic end of the continuum, with possible matrotrophic contributions of lipids intended for primarily structural functions. If one calculates the change in lipid and protein content in ovaries from fertilization to eyed larvae stage (i.e. just prior to parturition) for yellowtail rockfish, there is an estimated 21% reduction in weight and 16% energy loss. Net weight losses of 25–35% suggest no maternal nutrient inputs during gestation (i.e. lecithotrophy) whereas weight changes ranging from slight losses (e.g. to 10%) to net increases indicate matrotrophy (Wourms et al. 1988).

Respirometry and calorimetry measurements on three species of rockfishes, *S. melanops*, *S. schlegeli*, and *S. caurinus*, suggested some maternal transfer of energy during gestation where weight changes were −11, +22, and −21%, respectively (Boehlert and Yoklavich 1984; Boehlert et al. 1986; Dygert and Gunderson 1991). The comparable energy losses, based on calorimetry data, for the three rockfish species were 20, 7, and 34%, respectively. Our method of assessing changes in organic weight and energy content during ovarian matura-

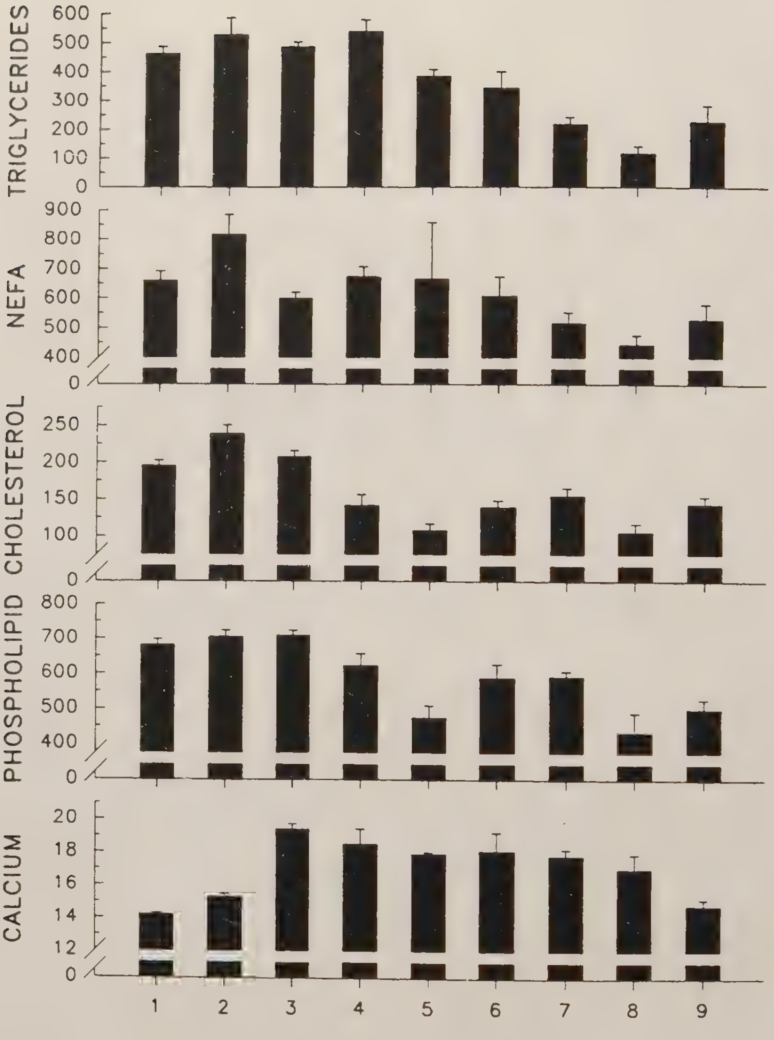

FIG. 5. Variation in serum lipids and calcium (vitellogenin surrogate) by OMS in adult female *S. flavidus* from April 1985 through April 1991. Values are means + SE in mg/dL for all variables except NEFA (μEq/L). See legend of Fig. 4 for OMS key.

tion, independent of calorimetry and respirometry, established *S. flavidus* values within the ranges established for other rockfish species considered to have some degree of matrotrophy (Wourms 1991).

Levels of phospholipids, cholesterol, and calcium (indicative of vitellogenin in females) in maternal *S. flavidus* serum during gestation were high relative to values found in male serum during the same period. This indicates matrotrophic contributions to embryonic nutrition in *S. flavidus*. For instance, lipids, particularly phospholipids, were increased in serum of the matrotrophic blenny *Zoarces viviparus* (Korsgaard and Petersen 1979) and the embiotocid *Cymatogaster aggregata* (deVlaming et al. 1983) during gestation.

If elevated serum calcium in yellowtail rockfish reflects vitellogenin levels, as found in other fish species (Oguri and Takada 1967; Yaron et al. 1977; Elliot et al. 1979; Hori et al. 1979), then vitellogenin transport during embryogenesis contrasts with data from a western Pacific congener, *Sebastes taczanowski* (Takemura et al. 1991). Vitellogenin did not occur in maternal serum of *S. taczanowski* during gestation. However, another viviparous teleost, *Gambusia affinis*, previously considered lecithotrophic (Wourms et al. 1988), has been shown to circulate vitellogenin during pregnancy (R. A. Wallace, C. V. Whitney Laboratory, St. Augustine, FL, pers. comm.).

A reproductive strategy of primarily lecithotrophic viviparity, supplemented by matrotrophy of certain components,

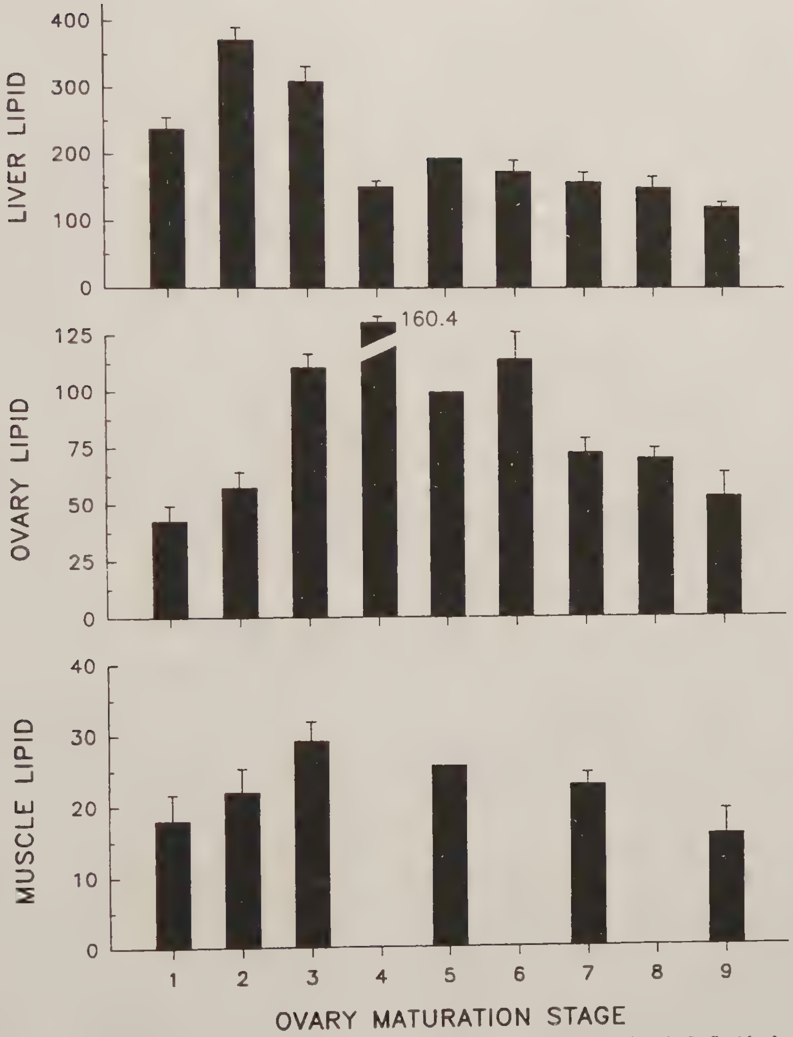

Fig. 6. Changes in total lipid concentration in liver, ovary, and muscle of adult female *S. flavidus* by OMS. Values are means + SE in mg/g fresh weight. See legend of Fig. 4 for OMS key.

would be beneficial to *S. flavidus*. Species inhabiting Pacific coastal areas of temperate North America must adapt to cycles of physical factors (e.g. temperature, currents) and biotic productivity dominated by upwelling of deep ocean water (Boje and Tomczak 1978). In most years, upwelling and associated productivity begin in March or April off central California (Bakun et al. 1974; Cushing 1978). During winter, when *S. flavidus* reproduce, upwelling is usually greatly reduced leading to scarce food supplies, although upwelling and productivity during this period do occur in some years (e.g. Bakun 1975). Supplemental matrotrophic processes would allow utilization of environmental productivity for reproduction during this time. Being primarily lecithotrophic, however, females can accumulate lipid reserves during the summer and early fall when prey is predictably abundant to support reproduction during the winter. Thus, *S. flavidus* employ lecithotrophy as an adaptive strategy in a predictable, yet cyclic environment to couple disparate time intervals of food abundance and reproductive development. This contrasts with other situations where lecithotrophy may be advantageous, such as with *Poeciliopsis*, where unpredictable environmental conditions and food supply are encountered (Thibault and Schultz 1978).

It is interesting that *S. flavidus*, a relatively fecund viviparous species with a long life span, would seem to adopt a reproductive nutritional strategy of committing lipids to ovarian development so early in the cycle (2–3 mo prior to fertilization) and not later when adequate nutrition and energy for female sustenance can be ensured. Poor nutrition and energy reserves can lead to increased susceptibility to disease and parasites (Ghittino 1989). Most viviparous species have small broods

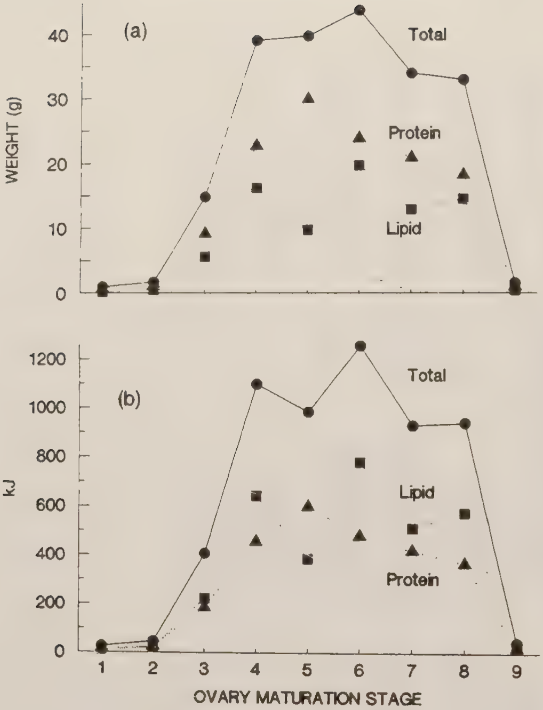

FIG. 7. Profiles of (a) quantities and (b) energy content of total organic weight, lipid, and protein in ovaries of standard female *S. flavidus* by OMS. Values are means adjusted for variation of size (ln (standard length)) by ANCOVA of females obtained from April 1985 through April 1991.

(Wourms et al. 1988 whereas yellowtail rockfish fecundity approximates 1 × $10^6$/female with a reproductive life span to 45 yr (Eldridge et al. 1991). In lean feeding years, retaining lipids in mesenteries and other tissues until fertilization or later would increase the prospects of maternal survival and greater production of progeny in future, more optimal years, perhaps at the expense of the present year-class. If inadequate energy reserves are available, some of the intraovarian embryos may subsist on nutrients from other resorbing embryos, as proposed by Boehlert et al. (1986) for *S. schlegeli*, and contribute to a smaller year-class. Year-class strength is highly variable in *Sebastes* populations on the west coast of North America and may be due, in part, to lower reproductive success of adult populations during years of lower food supply (Moser and Boehlert 1991).

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# Ecology and Conservation of Green Turtles in the Nearshore Waters of Waikiki Beach

by Russell K. Miya[1] and George H. Balazs[1]

The Hawaiian green turtle, *Chelonia mydas*, has been listed and protected under the U.S. Endangered Species Act since 1978. Equivalent legal protection is also afforded by the State of Hawai'i. Selected nearshore foraging and resting habitats in the main Hawaiian Islands have been a focus of research on this species. On O'ahu, sites such as Kane'ohe Bay, Kawela Bay, Maunalua Bay, and West Beach are among the important areas used by green turtles for such purposes (Balazs et al. 1987, Balazs and Pooley 1991). Additionally, in recent years, an area has been identified off Waikiki Beach where prominent sightings of turtles occur on a daily basis. The area fronts the Sheraton Waikiki Hotel (21°16'48"N, 157°49'59"W) and is unique because of the number of tourists swimming, snorkeling, and even sunbathing on air mattresses while the turtles swim and feed around them. In the past, Waikiki has not been a haven for sea turtles, although occasionally they were reported there. It would appear that only in the past 3-5 years has the number of turtles off Waikiki increased and their presence become more visible.

An effort was made in the present study to better define the ecology and conservation status of the aggregation of turtles fronting the hotel. Research was undertaken to gather basic information on several important aspects, including the environmental characteristics of the habitats used by the turtles for feeding and underwater resting, the approximate number of turtles present and their size classes, the daily feeding patterns and food sources, and any adverse impacts to the turtles, both from humans as well as from natural factors such as disease and shark predation.

A recovery plan to promote the biological recovery and long-term conservation of green turtles in the Hawaiian Islands has been prepared (NMFS 1992). The work that was undertaken off Waikiki is consistent with several recommendations for field research contained in the recovery plan.

## Methods

Between October 1990 and August 1991, 20 underwater surveys were conducted to determine the environmental characteristics of the study area, including foraging sites and resting habitats. This was accomplished by snorkeling in and around the general area where the turtles were seen. Visual surveys were conducted from the shoreline to observe (1) turtles foraging and (2) the characteristics of the nearshore and intertidal habitats. In addition, the study site was observed from the upper floors (usually a room on the 12th floor) of the hotel, providing an ideal vantage point for sighting and censusing turtles.

Capture methods consisted of (1) entrapment in large mesh nets previously used to safely sample turtles at other sites in Hawai'i and (2) capture by hand while skin diving. Once a turtle was captured it was tagged for long-term identification. Two different tags were used—a highly visible blue plastic tag and a tag made of the highly corrosion resistant alloy, Inconel. Two or three tags were applied to each turtle, depending on the size of the animal. Tagging sites consisted of the trailing edges of the front and rear flippers. Besides tagging, painted letters were applied to each turtle's carapace to facilitate short-term recognition from a distance.

Body measurements and weight were recorded for each turtle. Measurements included straight-line and curved carapace length, straight-line and curved carapace width, and straight-line plastron length. Other measurements included head width, right front flipper width, and tail length.

Food sources were determined by sampling the turtle's mouth shortly after capture, or by gently inserting a plastic tube lubricated with vegetable oil into the esophagus to the upper portion of the fore-stomach (crop). Seawater was then infused at a low pressure to flush food particles for collection and identification (Balazs 1980; in press).

## Results

### Environmental setting

Waikiki Beach is located on the south shore of the Island of O'ahu and extends from the Ala Wai Yacht Harbor to Diamond Head, a distance of about 3 km. It is, undoubtedly, the most visited beach in all the Hawaiian Islands and ranks among the best recognized tourist destinations worldwide. The number of beachgoers on any given day can reach into the thousands. One of two main areas, where tagging occurred, fronts the Sheraton Waikiki Hotel. This site is divided by an old seawall that extends seaward for about 30 m and curves toward Diamond Head, parallel to shore, for 20 m. This seawall was used in our capture efforts as a barrier to trap turtles by rapidly swimming out a net to form an enclosure while a turtle was seen feeding. Both sides of the seawall close to shore are shallow with a depth of 1-2 m. The majority of the bottom here consists of sand with some hard calcareous substrate. Patches of vertical reef start approximately where the seawall starts to curve.

A second site discovered during the course of the study that became a focus for tagging is located at 21°16'35"N, 157°49'35"W in water 3 m deep about 300 m off the Kapahulu seawall. The Kapahulu seawall is located 600 m east of the Sheraton Waikiki. This site, designated in our work as "Grace's Ledge," was ideal for hand capturing turtles frequently found resting in the recess of this limestone structure. Three other smaller recesses a short distance away were found to be used occasionally by turtles for resting.

On five occasions, surveys were made along the intertidal shoreline of Waikiki to look for fecal pellets. No pellets were encountered. This was considered an important find-

Table 1.—Body measurements and weights of 15 green turtles captured off Waikiki Beach.

G = Grace's Ledge, N = Natatorium, and S = Sheraton Waikiki Hotel

| Primary tag No. | Date and site | Carapace length (cm) Straight | Carapace length (cm) Curved | Plastron length (cm) | Weight (kg) |
|---|---|---|---|---|---|
| N840 | 4-26-91 (S) | 37.6 | 39.5 | 31.2 | 7.7 |
| N844 | 4-26-91 (S) | 42.0 | 45.0 | 33.5 | 10.9 |
| N535 | 11-15-90 (G) | 42.5 | 45.5 | 34.5 | 12.3 |
| N842 | 4-26-91 (S) | 42.9 | 46.0 | 33.8 | 10.9 |
| N776 | 3-28-91 (G) | 43.2 | 46.5 | 33.7 | 12.7 |
| N573 | 12-20-90 (N) | 43.7 | 47.0 | 34.7 | 13.6 |
| N741 | 3-15-91 (S) | 44.7 | 47.0 | 35.3 | 15.0 |
| N778 | 3-29-91 (G) | 48.9 | 53.0 | 40.2 | 16.4 |
| N570 | 12-14-90 (G) | 49.5 | 53.0 | 40.7 | 20.5 |
| N691 | 3-1-91 (S) | 49.9 | 53.3 | 39.7 | 21.4 |
| N781 | 3-29-91 (G) | 60.1 | 63.5 | 47.1 | 28.6 |
| Y47 | 12-14-90 (G) | 61.2 | 65.0 | 49.9 | 35.5 |
| N793 | 4-5-91 (S) | 61.3 | 65.2 | 49.5 | 32.7 |
| N744 | 3-15-91 (S) | 69.3 | 74.0 | 56.1 | 51.4 |
| N796 | 4-5-91 (S) | 80.7 | 86.2 | 64.4 | 81.8 |

Table 2.—Identification of dietary components flushed from four green turtles captured off Waikiki Beach.

| Primary tag No./ study site/date | Straight carapace length (cm) | Sample contents | % Composition |
|---|---|---|---|
| N691-Sheraton Waikiki 3-1-91 | 49.9 | *Spyridia filamentosa* | 30 |
| | | *Gelidium pusillum* | 30 |
| | | *Laurencia nidifica* | 20 |
| | | *Dictyota friabilis* | 10 |
| | | *Ulva fasciata* | 10 |
| | | *Lyngbya* sp. | Trace |
| | | *Ceramuim* sp. | Trace |
| | | Amphipods (commensural) | Trace |
| N741-Sheraton Waikiki 3-15-91 | 47.7 | *Pterocladia capillacea* | 80 |
| | | *Hypnea musciformis* | 15 |
| | | *Acanthophora spicifera* | 5 |
| | | *Ectocarpus indicus* | Trace |
| | | *Sargassum* sp. | Trace |
| N844-Sheraton Waikiki 4-26-91 | 42.0 | *Hypnea musciformis* | 45 |
| | | *Sargassum* sp. | 30 |
| | | *Ulva reticulata* | 15 |
| | | Paper | 10 |
| | | *Ectocarpus indicus* | Trace |
| N776-Grace's Ledge 3-28-91 | 43.2 | *Ulva fasciata* | 100 |
| | | Terrestrial plant material | Trace |
| | | Amphipods (commensural) | Trace |
| | | Unidentified spine | Trace |

ing because of the large number of beach users and the potential for negative public reaction if large numbers washed ashore (Balazs et al. 1990).

**Ecological aspects of turtles captured**

Netting efforts conducted on six occasions in front of the Sheraton Waikiki Hotel resulted in eight turtles being captured (Table 1). Six of the turtles were caught on the Sheraton (west) side of the seawall, and two were caught on the Diamond Head (east) side bordering the Royal Hawaiian Hotel. All netting attempts were conducted in the late afternoon because the number of turtles observed from the hotel room was consistently greater at that time of day. Six turtles were hand captured at Grace's Ledge (one turtle was caught twice), and one was caught in front of the Waikiki Natatorium. All turtles were captured during the day as nighttime efforts were not attempted. The straight carapace lengths of the 15 turtles captured ranged from 37.6-80.7 cm. Their weights ranged from 8-82 kg (Table 1). The largest turtle, the only adult captured, was determined to be a maturing male on the basis of its long, thick tail.

Stomach samples collected from four of the turtles resulted in the identification of several species of benthic algae (Table 2). Two of the three turtles captured in front of the Sheraton Waikiki contained *Hypnea musciformis*, a red alga introduced to the Hawaiian Islands from Florida in 1974 (Abbott 1987, Russell and Balazs, in prep.). One of the turtles at Grace's Ledge sampled for stomach contents was found to have been feeding exclusively on the green alga, *Ulva fasciata*. *Ulva fasciata* and *U. reticulata* were both highly visible species at the Sheraton Waikiki study site. Various other algae and related samples shown in Table 3 were identified from the external surfaces of the turtles.

Over the 10 months of this study, three turtles were found dead along Waikiki Beach. Two of these turtles died from obvious boat propeller slashes. The third turtle (tag N535), which was the first turtle tagged at Grace's Ledge, died from entanglement and forced submergence in a fisherman's gillnet. Identification of the stomach contents of the three turtles revealed that considerable foraging had taken place on *H. musciformis*, *Ulva* spp., *Codium* spp., and *Pterocladia capillacea* (Table 4).

Eight of the 15 turtles captured showed some evidence of external injury or abnormality, although in most instances they were minor. One turtle (tag N535) had obvious healed puncture marks from a threeprong (Hawaiian sling) spear on its head.

One of the turtles captured at Grace's Ledge (tag Y47) had been originally tagged in December 1989 after being found entangled in a fisherman's gillnet set in shallow water off the Kapahulu seawall. A Waikiki lifeguard rescued the turtle and turned it in to the Waikiki Aquarium. A few days later the turtle was tagged and transported for release by one of us (GHB) to Kawaikui Beach Park, about 8 km east of Waikiki on O'ahu's south shore. During the one year period following its release the turtle grew 3.6 cm in straight carapace length. This same turtle was recaptured a second time (again at Grace's Ledge) after 4 more months in the wild. The growth during this period was 1.2 cm in straight carapace length. These rates are relatively rapid compared to turtles residing at other sites thus far studied in the Hawaiian Islands (Balazs 1982).

Submergence intervals (breath-hold times) were recorded on two turtles that were meticulously observed from a room at the Sheraton Waikiki Hotel. Both turtles were foraging during this period. Their average submergence times were relatively short (1 min 46 sec, and 2 min 11 sec). Submergence times ranged from 35 sec to 3 min 30 sec (n = 32).

### Foraging habitat appraisal

Surveys conducted from shore and underwater demonstrated an abundance of various algae in the nearshore waters fronting the hotel. Algae that were highly abundant included *U. reticulata* and *U. fasciata*. An assortment of detached algae was also seen along the sand bottom adjacent to the seawall. Loose algae collected were identified as *Codium* spp., *Sargassum* spp., and *H. musciformis*.

The number and frequency of turtles sighted from shore were always greater during late afternoon to early evening than in the morning and early afternoon. Also, the number of turtles sighted was greater during these times when high tides occurred.

Underwater surveys taken at Grace's Ledge indicated that there were no foraging habitats in the immediate vicinity.

Table 3.—Identification of samples scraped from the external surfaces of three green turtles off Waikiki Beach.

| Primary tag No./ study site | Straight carapace length (cm) | Sample contents | % Composition |
|---|---|---|---|
| N741-Sheraton Waikiki 3-15-91 | 44.7 | *Sphacelaria furcigera* | 90 |
| | | *Achrochaetuim* sp. | 10 |
| | | *Chaetomorpha gracilis* | Trace |
| | | *Lyngbya* sp. | Trace |
| | | Round worm | |
| N744-Sheraton Waikiki 3-15-91 | 69.3 | 5 *Ozobranchus branchiatus* on front flipper | |
| Y47-Grace's Ledge 12-14-90 | 62.4 | 1 *O. branchiatus* in mouth | |

### Resting habitat appraisal

Hawaiian green turtles spend most of their time foraging, resting on the bottom, and swimming to the surface to breathe. The turtles' resting periods are often spent at the bottom in or near caves, reef outcroppings, ledges, or crevices. Two important resting locations were discovered in this study—Grace's Ledge and a site known as Canyons. Canyons is located about 400 m off Fort DeRussy in Waikiki, in water 10 m deep at 21°16'38"N, 157°50'32"W. This site was brought to our attention by personnel of the vessel Explorer operated by Atlantis Reef Divers. The Explorer visits this site daily to conduct scuba diving with tourists and other clients. In addition to resting motionless on the bottom, turtles have been seen at this location being "cleaned" by surgeon fish and wrasses. Additional studies are needed for a better understanding of the significance of this behavior and what factors contribute to the establishment of discrete cleaning stations.

John Wilson, a video specialist and professional diver on the Explorer, reported the

Table 4.—Identification of dietary components from three green turtles found dead on Waikiki Beach.

| Primary tag No./ cause/date | Straight carapace length (cm) | Sample contents | % Composition |
|---|---|---|---|
| Propeller slashes 10-9-90 | 53.0 | *Ulva reticulata* | 90 |
| | | *Acanthophora spicifera* | 5 |
| | | *Amansia glomerata* | Trace |
| | | *Champia parvula* | Trace |
| | | *Gelidiella acerosa* | Trace |
| | | *Gracilaria coronopifolia* | Trace |
| | | *Lyngbya majuscula* | Trace |
| Z227 Gillnet mortality 12-17-90 | 42.5 | *Hypnea musciformia* | 30 |
| | | *Pterocladia capillacea* | 30 |
| | | *Ulva reticulata* | 25 |
| | | *Codium edule* | 15 |
| | | *Acanthophora spicifera* | Trace |
| Propeller slashes 4-3-91 | 50.0 | *Ulva fasciata* | 50 |
| | | *Pterocladia capillacea* | 40 |
| | | *Amansia glomerata* | 10 |
| | | *Bryopsis pennata* | Trace |
| | | *Polysiphonia howei* | Trace |
| | | Cellophane | Trace |
| | | Fishing line | Trace |

underwater sighting of three tagged turtles at Canyons. Two of these turtles (tags N842 and N844) had been netted in front of the Sheraton Waikiki, and the other (tag N570) had been hand-captured at Grace's Ledge.

### Adverse impacts to the population

Several potential and actual impacts to the turtles off Waikiki were identified in this study, in addition to the ones previously mentioned relating to boat collisions and gillnets. Plastics and other synthetic debris were commonly seen along the beach and in the nearshore waters. Buoyant litter of this nature can be ingested by or can entangle sea turtles and have harmful effects (Balazs 1985). One of the turtles (tag N844) sampled off the Sheraton Waikiki was found to have eaten paper (Table 2).

Disease and predation by sharks were not identified in this study as major factors. On one occasion, a turtle was observed with a section of its carapace missing, but healed. This may have resulted from impact by a boat, or from shark attack.

During the course of the study only one turtle was sighted with fibropapillomas (tumors). This turtle was seen at Canyons and documented on videotape by John Wilson as being in poor condition because of emaciation and numerous large tumors. The turtle was subsequently found dead—washed ashore at Magic Island near Ala Moana Beach Park, immediately west of Waikiki Beach. The prevalence of tumors on green turtles is substantially greater at several other locations on O'ahu and elsewhere throughout the Hawaiian Islands. For example, in Kane'ohe Bay an estimated 50% of the turtles are afflicted with this disease (Balazs and Pooley 1991).

Other potential adverse impacts from humans were discovered at Grace's Ledge during November 1990. An illegal mooring buoy was found attached to the ledge by a chain and rope, immediately over the turtle resting site. Three possible consequences could have resulted from this mooring had it not been reported to authorities and subsequently removed. First, the mooring line could have entangled a turtle, causing it to drown. Secondly, power boats using the mooring increased the likelihood of collision with a turtle. And lastly, the buoy served to "mark" the ledge thereby attracting visitors to it and increasing the level of disturbance.

### Conclusions

During this 10-month study 15 turtles were captured, tagged, and released off Waikiki Beach. Only one species, the green turtle, was encountered. Green turtles feed in shallow waters within 100 m of shore, and were commonly seen engaged in this activity in front of the Sheraton Waikiki. Food sources utilized off Waikiki Beach consisted primarily of the benthic algae *U. fasciata*, *U. reticulata*, *H. musciformis*, *P. capillacea*, *Spyridia filamentosa*, and *Gelidium pusillum*. Sizes of the turtles tagged ranged from 37.6 cm (8 kg) to 80.7 cm (82 kg). Resting habitats for turtles were identified at Grace's Ledge off the Kapahulu seawall and at Canyons off Fort DeRussy. None of the turtles tagged and released had signs of disease, although one turtle was seen with fibropapillomas, and subsequent to this study a few others with the disease have been reported in the area. The findings from this study lead to the tentative conclusion that the green turtle population off Waikiki Beach is relatively large (perhaps > 100 individuals), and in a generally healthy condition. However, adverse impacts especially from gillnet fishing and boat traffic are causes for concern that should be addressed. Efforts need to be made to enhance the protection of these turtles and the habitats upon which they depend. The educational and ecotourism aspects of viewing turtles in a benign fashion, from both above and below the water, should be promoted wherever possible.

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## CHAPTER 4

# Deepwater Demersal Fish

*Robert B. Moffitt*

## I. INTRODUCTION

Demersal fisheries are a very important component of total world catches. The FAO 1987 Yearbook of Fishery Statistics (FAO, 1989) reports total landings of marine finfish equaling 68 million metric tonnes (t). The three major species groups of demersal finfish - flounders, cods, and redfishes - account for 20 million t or just under one third of the total. By comparison, tuna and billfish landings were reported at 3.4 million t for the same year.

The majority of the demersal finfish yields are from the fisheries on wide continental shelves and slopes (*e.g.* the Bering Sea and Patagonia) at depths of 50 to 500 m. Unfortunately, shallow reef areas around the Pacific islands tend to drop quite rapidly to abyssal depths, leaving relatively little habitat area for deep-slope species.

Snappers (family Lutjanidae) and groupers (family Serranidae) (included in the redfishes group mentioned above) are important components of the demersal fisheries catch throughout the tropical and temperate oceans. In general, the shallower (<100 m) dwelling members of these families are of relatively small size and, though commercially important, comprise only a minor portion of the catch at these depths (Munro, 1987).

Finfish catches on the deep (100-500 m) slopes of the Pacific islands, however, are dominated by a few species of snappers and groupers which tend to be of larger size than shallower species (Munro, 1987). These deep-slope species have not been a major component of the traditional, subsistence fisheries in the Pacific areas, but because of their demand as a high-quality product for tourist and export markets, they have become an important component of developing commercial fisheries.

## II. LIFE HISTORY AND POPULATION BIOLOGY

### TAXONOMY

The taxonomy of the deep slope species is relatively stable; recent reviews and keys to species are in Anderson (1987) and Randall (1987). The major area of taxonomic contention is found in the snapper genus *Etelis*, where *E. carbunculus* (Cuvier 1828) is in current usage for both the small sized North Pacific individuals, such as the 26-63 cm fork length (FL) fish found in Hawaiian waters (Everson, 1986), and the much larger South Pacific individuals, such as those reaching 112 cm FL in Vanuatu (Brouard and Grandperrin, 1984). The question remains unanswered as to whether one or two species are involved. Support for the two-species hypothesis includes the uniquely bimodal length-frequency distributions reported by Lokani *et al.* (1990) and King *et al.* (*in prep.*) for fish from Papua New Guinea and Western Samoa, respectively.

## DISTRIBUTION

Most of the deep slope demersal fish species are widely distributed throughout the central, western and South Pacific although species richness tends to decline with distance from the Indo-Pacific faunal centre, leaving areas like Hawaii with somewhat fewer species. Table I lists many of the more commonly caught species from several families.

Snappers of the subfamilies Etelinae and Apsilinae and groupers of the subfamily Epinephelinae are the most important elements of this fishery both in terms of landings (ranging from 70 per cent to over 90 per cent of the total catch) and value (because of high quality and marketability). Biological discussions and yield estimates presented in this chapter will be restricted to members of these two families.

Although the majority of the more important species are wide ranging, their relative contribution to the catch varies considerably with location. In Hawaii, *Pristipomoides filamentosus* (Valenciennes 1830) is the most abundant species, comprising about 20-40 per cent of the demersal catch (Moffitt, 1980; Polovina and Moffitt, 1980; Ralston and Kawamoto, 1987; 1988). In the Marianas, on the other hand, *P. zonatus* (Valenciennes 1830) is the most abundant species, where it contributes over 50 per cent of the total deepwater demersal catch (Polovina, 1985; Ralston and Williams, 1988). In many other areas, *Etelis* spp. dominate the deepwater finfish catch (King *et al.*, *in prep.*; Grandperrin and Kulbicki, 1988; Lewis *et al.*, 1988; Nath and Sesewa, 1990).

## HABITAT

Adults and large juveniles of the deepwater snappers and groupers tend to be caught over high relief features (e.g. pinnacles or steep slopes) at depths of 100-500 m, indicating a preference for this type of habitat. Submersible observations of both natural (Ralston *et al.*, 1986) and artificial habitats (Moffitt *et al.*, 1989) suggest that snappers (specifically those of the genus *Pristipomoides*)

**Table I. List of common deepwater demersal fish species.**

Family Lutjanidae

*Aphareus rutilans* (Cuvier 1830)
*Aprion virescens* (Valenciennes 1830)
*Etelis carbunculus* (Cuvier 1828)
*E. coruscans* (Valenciennes 1862)
*E. radiosus* (Anderson 1981)
*Paracaesio caerulea* (Katayama 1934)
*P. kusakarii* (Abe 1960)
*P. stonei* (Raj and Seeto 1983)
*P. xanthura* (Bleeker 1869)
*Pristipomoides auricilla* (Jordan, Evermann, and Tanaka 1927)
*P. filamentosus* (Valenciennes 1830)
*P. flavipinnis* (Shinohara 1963)
*P. multidens* (Day 1870)
*P. sieboldi* (Bleeker 1857)
*P. zonatus* (Valenciennes 1830)

Family Serranidae

*Cephalopholis aurantia* (Valenciennes 1828)
*C. igarashiensis* (Katayama 1957)
*C. sexmaculata* (Ruppell 1830)
*C. sonnerati* (Valenciennes 1828)
*Epinephelus chlorostigma* (Valenciennes 1828)
*E. lanceolatus* (Bloch 1790)
*E. morrhua* (Valenciennes 1833)
*E. septemfasciatus* (Thunberg 1793)
*Saloptia powelli* (Smith 1963)
*Variola louti* (Forsskal 1775)

Family Lethrinidae

*Gymnocranius euanus* (Gunther 1879)
*G. griseus* (Schlegel 1844)
*Lethrinus rubrioperculatus* (Sato 1978)

Family Carangidae

*Caranx lugubris* (Poey 1861)
*Elegatis bipinnulatus* (Quoy and Gaimard 1824)
*Seriola dumerili* (Risso 1810)
*S. rivoliana* (Valenciennes 1833)

Family Scombridae

*Gymnosarda unicolor* (Ruppell 1836)

form loose aggregations of up to at least 50 individuals around such high relief features.

Brouard and Grandperrin (1984) and Ralston and Williams (1988) list depth ranges for many of the deepwater demersal species. In short, carangids, lethrinids, and many epinephelids are shallower dwellers (<120 m), *Pristipomoides* spp. and some epinephelids are found at intermediate depths (120-240 m) and *Etelis* spp. and a few epinephelids are deeper dwellers (>240 m).

Sundberg and Richards (1984) report that individual fish size increases with depth when all species are pooled. Ralston and Williams (1988) found, however, that, within species, size is poorly correlated with depth, indicating that increases in mean fish size with depth are due to changes in species composition, not depth stratification by size for individuals of any particular species.

Some species may not be restricted to deep slope, high relief habitat. Evidence suggests that individuals of *P. filamentosus* in Hawaii, for example, undergo a diurnal migration from deeper daytime high relief areas at depths of 100 to 200 m, to shallower night flat shelf areas at depths of as little as 30 to 80 m (Moffitt, 1980). This behavior has not been demonstrated for other species or areas. In contrast to the snappers, deep slope groupers are probably solitary and territorial in nature, as are their shallower dwelling congeners (Parrish, 1987; Shapiro, 1987).

Although adult habitat for most of the deep slope snappers and groupers is well known, the nursery grounds for newly settled and young juveniles have not been identified. Recent studies in Hawaii suggest that juveniles may utilize the flat, featureless areas of banks, avoiding the high relief areas where larger fish (potential predators) accumulate (Parrish, 1989; Moffitt and Parrish *unpubl. data*).

Large concentrations of juvenile opakapaka, *P. filamentosus*, have been found on the featureless, silty bottom at 70-100 m depths off of Kaneohe Bay, Oahu. At this site, they dominate the rod and reel catch (well over 90 per cent of the catch). They apparently utilize this area for a period of about 6-9 months (FL 7-20 cm), then move deeper to higher relief areas.

During their stay within this habitat, juvenile opakapaka appear to undertake a diurnal migration similar to that described above for the adults. A single sonic tag track showed a 19 cm FL individual migrated cross-shelf from a daytime location at 85 m depth to a night time location at 75 m depth. These movements occurred consistently at dawn and dusk over the 5 day life of the tag (Moffitt and Parrish, *unpubl. data*).

Similarly, six newly settled specimens (ca. 25 mm standard length (SL)) of Hawaii's deep slope grouper, *Epinephelus quernus* (Seale 1901), have been collected from lobster traps set at 40-80 m on flat sand and mud areas off Kaneohe Bay, Oahu and off Maro Reef in the Northwestern Hawaiian

Islands. When captured, these specimens had pelagic coloration (translucent pink with darker vertical bars) and a black "flag" on the longest dorsal spine when captured. Two specimens transformed to juvenile coloration (black with white dots) and lost the "flag" on the dorsal spine within 4 days of shipboard captivity.

## FEEDING

Studies on the feeding habits of deepwater snappers and groupers have been hampered by the great depths involved. The fish tend to regurgitate stomach contents during hauling and frequently are badly embolized with their stomachs completely everted (Seki and Callahan, 1988). Fortunately, some material often remains in the mouth or in the gill rakers, allowing at least a qualitative analysis of prey items. Feeding of both snappers and groupers undoubtedly occurs at the deep-slope, high relief features where they are hooked, but distance of feeding off the bottom is difficult to determine.

Fishermen report that groupers are generally hooked on the bottom, whereas snappers can be caught either on the bottom or, in many cases, several meters above the bottom. Dietary studies support the differences between these families, with benthic fish and crustaceans being important prey items for species of both families and pelagic urochordates (e.g. *Salpida* spp., *Pyrosomida* spp.) being important prey items for many species of *Pristipomoides* (Kami, 1973; Oda and Parrish, 1981; Seki, 1984; Parrish, 1987; Seki and Callahan, 1988).

## REPRODUCTION

Reproductive strategies differ greatly between the two major families included in this chapter. Studies have indicated that deepwater snappers are serial spawners able to spawn several times over a prolonged breeding season (Min *et al.*, 1977; Ralston, 1981; Everson, 1984; Kikkawa, 1984; Grimes, 1987). Although the number of spawning episodes per season has not been established for any species, ovaries typically contain three size classes of oocytes (Grimes, 1987). Ova size-frequency modes, however, are likely unrepresentative of spawning frequency in serial spawners (Hunter and Goldberg, 1980; DeMartini and Fountain, 1981).

Large female *E. carbunculus* in Hawaii develop ripe ova earlier in the breeding season and remain in breeding condition longer than those of smaller individuals (Everson, 1984), suggesting that larger females spawn more batches than smaller ones. Analysis of gonosomatic indices, coupled with visual staging of ova, suggests that deepwater snappers spawn in the summer (May to September in the North Pacific (Everson, 1984; Kikkawa, 1984; Ralston and

Williams, 1989; Everson *et al.*, 1989) and November to May in the South Pacific (Brouard and Grandperrin, 1984)).

Sexual maturity is attained at approximately 50 per cent of maximum length for deepwater species (Grimes, 1987). Fecundity for those species examined increases with fish size and reportedly ranges from 300,000 to 2,000,000 eggs, depending on size and species (Min *et al.*, 1977, Everson 1984, Kikkawa 1984). However, realistic estimation of annual egg production is very difficult, because deepwater snappers are serial spawners with an unknown number of spawning episodes per season.

Reproduction of groupers differs markedly from that of snappers. Although data on the reproductive biology of Pacific deepwater species are lacking, all grouper species studied to date have been shown to be protogynous hermaphrodites (Shapiro, 1987).

The general pattern of grouper reproduction presented by Shapiro (1987) is as follows. The breeding season is abbreviated (peaking for 1-2 months) with an unknown number of spawnings per individual male or female. Spawning often takes place in large spawning aggregations, during which time stocks become unusually susceptible to fishing pressure. Fecundity for the deep sea species has not yet been determined, but ranges from 100,000 to 5,000,000 in other grouper species (Shapiro, 1987). The stimulus for sex change from female to male is unknown and could be related to size, age, or social interactions.

## LARVAL BIOLOGY AND ECOLOGY

Relatively little is known of the taxonomic relations or ecology of deep-slope snapper and grouper larvae. Both snappers and groupers have pelagic eggs and larvae. But, snapper and grouper larvae are a minor component of larval fish catches, contributing to the lack of ecological information on these species. Larvae of both families avoid surface waters during the day but become more evenly distributed vertically at night. Larvae of eteline snappers are generally found in oceanic waters, in contrast to larvae of other snappers that are most abundant over shelf waters. Grouper larvae are also most abundant over shelf waters, but as identification to species is not currently possible, the horizontal distribution of larvae of deepwater species is not known (Leis, 1987). Studies are in progress to identify the larvae of several species of *Etelis, Aprion,* and *Pristipomoides* (Leis, 1987). Leis (1987) reports fertilized eggs of *P. seiboldii* (Bleeker 1857) are 0.88-0.98 mm in diameter and hatch in about 36 hours at temperatures of 23-25° C.

## GROWTH

The most commonly used model for expressing growth in fisheries studies is the von Bertalanffy growth formula, which for growth in length takes the form:

$$L_t = L_\infty (1-e^{-K(t-t_0)})$$

where $L_t$ is the predicted length at age t, $L_\infty$ is the asymptotic length, K is the growth constant, and $t_0$ is the hypothetical "age" where the fish is at zero size. Estimates of growth parameters may be obtained through one of three basic sources, tag and recapture techniques, analysis of length-frequency distributions, or interpreting temporal markings on hard parts such as scales, vertebrae, and otoliths (Manooch, 1987). Various methods are found for utilizing each data source and each method has its own strengths and weaknesses.

Tag and recapture techniques give the most direct information on growth. Fish are measured when first caught, tagged with noticeable marker and released. When recaught the fish are measured again and the increase in length between marking and recapture is equated to growth. Jones (1979) reviews tagging materials and methods. In practice, growth rates obtained in tag and recapture studies are minimum growth rates, as fish are often stressed by capture, handling, and tagging operations resulting in a period of less than optimum growth. Tag and recapture studies have not been conducted on Pacific deepwater demersal species, and would be particularly problematic because these fish are usually near death from damage caused by their expanding gas bladder when brought to the surface.

The various methods of analysing length-frequency distributions rely on distinguishing length modes from large representative samples that are correlated to age classes (Pauly and Morgan, 1987). The Petersen method (Petersen, 1892) assigns ages to the multiple length-frequency peaks in a single large sample, whereas the Modal Class Progression Analysis method (George and Banerji, 1964) links length-frequency peaks from several samples taken at known time intervals. There are several computer programs available that assist in modal identification and parameter estimation (Mathews, 1974; Skillman and Yong, 1976; McNew and Summerfelt, 1978; Schnute and Fournier, 1980), including the now popular Electronic Length-Frequency Analysis (ELEFAN) method developed by Pauly and David (1981).

The benefits of using length-frequency analysis for growth estimation include the ease of data collection (often obtainable from existing catch data) and the lack of required technical skills for processing. On the negative side, several conditions must be met for meaningful results to be obtained. The sample must be representative of the size distribution of the stock and not biased by gear selectivity or varying size distribution by depth of capture. Best results are obtained from species with short breeding seasons and fast growth. In long-lived species, the older age class modes often overlap as they near asymptotic length. This overlap leads to an underestimate of the number of year classes involved such that, while $L_\infty$ estimates may be accurate, K is overestimated.

Unfortunately, deepwater snappers and groupers are long lived, slow growing and, at least in snappers, have prolonged breeding seasons, making them poor candidates for length-frequency analysis. Few studies have applied these methods to Pacific deepwater demersal species (Manooch, 1987). Pauly and Ingles (1981) obtained estimates of growth parameters using ELEFAN for *Epinephelus sexfasciatus* (Valenciennes 1828) from the Philippines ($L_\infty$=309 mm standard length (SL), K=0.510) and *Plectropomus leopardus* (Lacepede 1802) from Australia ($L_\infty$=647 mm total length (TL), K=0.250), but Langi (1990) determined that ELEFAN procedures were inappropriate for three species of snappers, *P. flavipinnis* (Shinohara 1963), *P. filamentosus,* and *E. coruscans* (Valenciennes 1862), from Tonga.

Otoliths (sagittae) have been the most commonly used hard part in fish growth determinations and the only one used to date for tropical deepwater snappers and groupers. In temperate regions, where fish growth rates vary seasonally, annual marks are formed on otoliths. These increments are often easy to observe after minimal otolith preparation and low-powered magnification. Annular increments are also reported for some tropical species (Loubens, 1978; Morales-Nin and Ralston, 1990) including some individuals of *P. zonatus* and *P. filamentosus* (Uchiyama and Tagami, 1984; Ralston and Williams, 1988) but, unfortunately, are not easily distinguishable even when present.

Pannella (1971; 1974) reported that daily growth increments could be discerned on fish otoliths, even in tropical species. Since that time otoliths of several deepwater tropical species have been examined using light microscopy and "daily" increments enumerated for age and growth determination (Ralston and Miyamoto, 1983; Brouard and Grandperrin, 1984; Uchiyama and Tagami, 1984; Radtke, 1987; Ralston and Williams, 1988).

Although very precise age estimates can be obtained under optimum conditions, several problems do arise when enumerating otolith daily growth increments. The shape and size of deepwater snapper and grouper otoliths do not lend them to whole mounting for microscopic increment enumeration. Instead, otoliths are generally embedded in plastic resin and thin sectioned (<1 mm) with a low-speed saw such that the center of the otolith (referred to as the "nucleus" or "focus") and the postrostral tip are included in the section.

Comprehensive increment counts are difficult to obtain in sections of deepwater snapper and grouper otoliths, because large areas are often cloudy, the degree of cloudiness varying with the individual preparation and species involved. Based on the assumption that cloudy areas are caused by deficiencies in preparation, the increment width method (Ralston and Miyamoto, 1983; Ralston, 1985; Ralston and Williams, 1989) was developed. In this method, increment widths are measured in several small sections along the axis of the otolith preparation and the total number of increments estimated through integration. Only areas where increments are clearly defined are utilized. Using

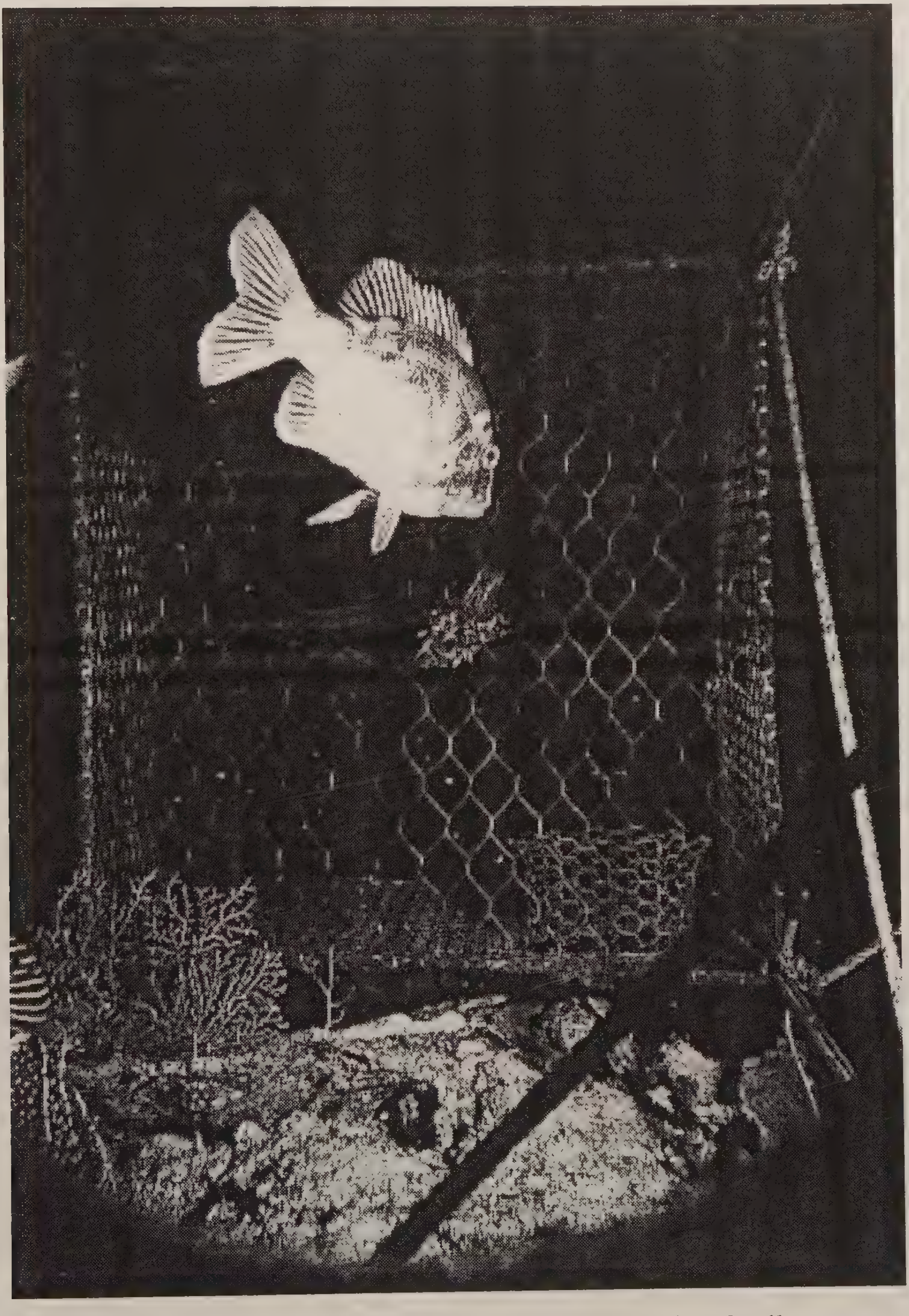

Figure 1. *Pristipomoides multidens* attracted to a trap set for *Nautilus* spp. at 270 m. (Photograph kindly provided by Bruce Saunders.)

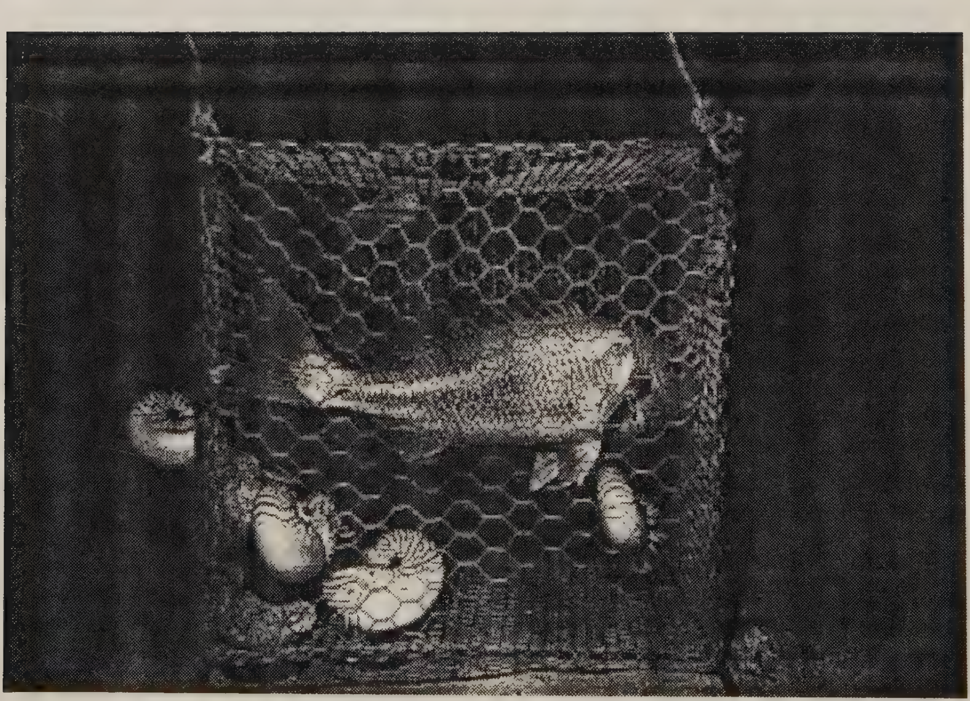

Figure 2. *Gnathodentex mossambicus* circling a baited trap at 167 m. (Photograph kindly provided by Bruce Saunders.)

scanning electron microscopy (SEM), however, Morales-Nin (1988) and Morales-Nin and Ralston (1990) have shown that the cloudy areas on the otoliths of some tropical species, including the shallow water snapper, *Lutjanus kasmira* (Forsskal 1775), are actually areas of slow growth with increments too narrow to be distinguished with light microscopy. They suggest that otoliths of prospective species be first examined using SEM, then, if all increments are wide enough to resolve under light microscopy, future otoliths could be analysed by either whole counts or the increment width method for age estimation of that species (Morales-Nin and Ralston, 1990).

Even when precise counts are obtained, verification of the temporal nature of the increments and their continued deposition for all ages of fish must be obtained. Evidence suggests increments are indeed daily in nature, but that by maturation (at about 3 years for *Pristipomoides* spp.) breaks appear in the daily deposition of increments making counts inaccurate (fewer increments counted leading to higher estimates of K) (Ralston and Miyamoto, 1983; Uchiyama and Tagami, 1984). This being true, estimates of K may be biased either by including mature fish in the sample, which will have fewer increments than days of age, leading to an overestimate of K, or by restricting the sample to juvenile fish and extrapolating growth rates for larger fish.

Familial characteristics have been observed in the relationships of various growth parameters (Beverton and Holt, 1959; Cushing, 1968; Pauly, 1980). Using the growth performance index (Ø') method of Pauly and Munro (1983), Manooch (1987) summarized the available snapper and grouper growth information. He found that snapper and grouper data overlapped greatly and could not be separated statistically. The resulting formula for pooled species of both families was: $\log_{10}(K) = 1.098 - 0.658 \log_{10}(L_\infty)$ with standard error estimates of 0.066 and 0.183 for the slope and intercept, respectively. Manooch (1987) reported mean values for maximum age of 10.49 years for lutjanids and 17.00 years for serranids with corresponding mean K values of 0.203 and 0.218 per year, respectively. Calculation of Ø' could be used to determine growth estimates if data from future studies fall within a reasonable range.

## MORTALITY

The instantaneous total mortality rate from all causes (Z) measures loss of individuals from the population. It is subdivided into two additive components, fishing mortality (F) and natural mortality (M), such that $Z = F + M$. In general total mortality is measured in one of three ways: 1) though tag-and-recovery methods (Ricker, 1975), 2) by measuring survivability of an age specific cohort over time (Gulland, 1955), and 3) by designating cohort sizes from a single sample using existing age-length information (Gulland, 1955).

As previously mentioned, capture, handling and tagging procedures stress fish and can cause an unknown increase in mortality. This is particularly true in the deepwater snappers and groupers where expanding gas bladders result in everted stomachs and potential internal damage. Grimes *et al.* (1983) developed a technique using detachable hooks to tag deepwater fish without bringing them to the surface. Although this method works well for monitoring fish movement, where small numbers of tag recovery can be sufficient, it does not work well for mortality (or growth) estimation. Problems stem from lack of knowledge as to species and size of tagged fish and unknown levels of additional mortality, both real (due to infection or impaired feeding) and apparent (due to sloughing of tags). In tank studies, Shiota (*unpubl. data*) tagged the shallow water snapper, *Lutjanus kasmira*, with varying types of detachable hook tags and observed over 50 per cent tag loss within 10 days regardless of tag type.

An important variation of the third method involves analysis of a single length-frequency distribution to estimate the ratio of Z/K (Wetherall *et al.*, 1987). An independent estimate of K allows separation of the ratio to obtain an estimate of Z. Separation of Z into its two components can be very difficult requiring a good time series of Z and fishing effort information. When length-frequency samples are obtained from unfished populations, however, natural mortality estimates are obtained since Z then equals M.

The Wetherall method has been used for estimating M (and $L_\infty$) for many deepwater snapper and grouper species (Brouard and Grandperrin, 1984; Ralston, 1987; Ralston and Williams, 1988). Care must be taken, to ensure the population under study is in equilibrium. Somerton and Kobayashi (1991, *in prep.*) ran a simulation model showing considerable bias in Z/K and $L_\infty$ values with disruption of equilibrium due to changes in F or recruitment (R). They suggest that equilibrium conditions should be verified by comparing length-frequency distributions from several consecutive years with a Chi-square test before relying on estimates derived from the Wetherall method.

Natural mortality can also be predicted empirically due to its relationship to von Bertalanffy growth parameters K and $L_\infty$ and the mean environmental temperature (T) (Pauly, 1980):

$$\log M = 0.0066 - 0.279 \log L_\infty + 0.6543 \log K + 0.4634 \log T.$$

Ralston (1987) suggests that in this relationship the value of K is of prime importance and that the addition of terms relating to $L_\infty$ and T provide little independent information. Therefore, good estimates of K are all that are needed for a good prediction of M. For snappers and groupers, Ralston found this relationship to be $M = 0.0189 + 2.06K$.

## III. RESOURCE ASSESSMENT

Most of the recent studies on deepwater demersal fish have focused on resource assessment. In fisheries where a long time series of catch and effort data is available, estimates of maximum sustainable yield (MSY) can be obtained using surplus production models. The Schaefer model has been applied to the multispecies deep-slope demersal fishery in Hawaii, resulting in an estimated MSY of about 0.27 $t.nmi^{-1}$ of 200 m isobath (Ralston and Polovina, 1982).

Unfortunately, a sufficiently long time series of data is not available for other Pacific Island areas because of the undeveloped or recently developed nature of the fishery in these areas. Thus, surplus production models cannot be applied, and alternate assessment methods must be sought.

Three such methods have been applied recently to tropical Pacific deepwater snappers and groupers. These methods are 1) the Gulland method (Gulland, 1969) which estimates MSY as a fraction of the product of M and unexploited exploitable biomass ($B_0$), 2) the Pauly method (Pauly, 1983) which estimates MSY as a function of fish weight, and 3) the Beddington and Cooke (1983) modification of the Beverton-Holt equation estimating MSY as a function of $B_0$, the ratio of M to K and the age at recruitment to the fishery ($t_r$). In all three approaches, estimates of MSY rely on first estimating $B_0$ and other biological parameters (see Polovina and Ralston, 1986).

## BIOMASS

Depletion studies have been used to obtain estimates of $B_0$ of deepwater snappers and groupers. Typically a small, isolated, virgin fishing area is intensively fished until a noticeable reduction in catch rates has been achieved (Polovina, 1986). If the period of depletion is short (< 9 mo), the catch per unit effort (CPUE) data are regressed on the cumulative removed biomass to obtain estimates of catchability (q) and $B_0$ following the Leslie model (Ricker, 1975). When the period of fishing is greater than 9 mo, these same estimates are obtained by applying the Allen depletion method (Sainsbury, 1984) which requires an estimate of M to estimate q, $B_0$ and mean recruitment (R).

Estimates of q and $B_0$ obtained by these methods are specific to the study area involved and are best standardized to a measure of area to allow comparison with other studies. The most frequently utilized standardized area unit is the length of 200 m isobath (Ralston and Polovina, 1982). Results obtained for several Pacific islands countries are summarized in Polovina *et al.*, (1990). Interestingly, estimates of $B_0$ for seamounts have been considerably greater than those for island fishing grounds: a median value of 2.7 $t.nmi^{-1}$ of 200 m isobath (range 1.4 to 8.5) versus 0.7 (range 0.2 to 2.3), respectively. Ralston (1988) also noted that the deepwater demersal fish off seamounts in the Marianas were heavier and more robust than those from other locations.

## YIELDS

Estimates of MSY for many of the Pacific islands countries by using the Gulland, Pauly, and Beddington-Cooke methods are summarized in Polovina *et al.* (1990). The estimates are expressed as the ratio of MSY to $B_0$ and range from 0.06 to 0.34, depending on the method used, the country of data origin, and the estimate of M applied. Based on the median values estimated for $B_0$ for seamount and island fishing areas considered individually, MSY values range from 0.16 to 0.92 $t.nmi^{-1}.yr^{-1}$ for seamounts and from 0.04 to 0.27 $t.nmi^{-1}.yr^{-1}$ for island areas.

Total MSY for individual countries are calculated as the product of MSY per nautical mile of 200 m contour and the estimated length of 200 m contour for that country. Landings for Tonga and Fiji in 1988 exceeded estimated MSY levels (Polovina *et al.*, 1990). This does not mean, however, that the current level of fishing is in excess of the level of fishing that would produce MSY.

It is suggested that MSY is achieved at levels of fishing where $F = M$ (Francis, 1974; Beddington and Cooke, 1983; Polovina, 1987). Estimates of F for both Tonga and Fiji (Polovina *et al.*, 1990) fall within the range of M estimates for snappers and groupers (Ralston, 1987), which suggests that stocks probably are not yet overfished and landings in excess of MSY are likely due to a "fishing down" process and will continue to decline at current fishing levels until an equilibrium yield is obtained.

## IV. FISHERIES DESCRIPTION

In general, traditional demersal fishing in the Pacific Islands has been concentrated on the shallow (<30 m) reef areas, with fishing in deeper waters targeting tunas, mackerels and other pelagic fishes (Dalzell, 1990). The deepwater demersal fisheries of most Pacific islands countries are either in the pre-development, survey stage or in early stages of commercial development. Hawaii is a notable exception with a 50 year history of commercial bottom fishing.

The market for deep slope demersal fish is a fresh fish market, so fish are iced and fishing trips are limited to about 10 days. Fishing fleets differ from country to country in the size of vessels and the level of technology utilized to locate fishing grounds and retrieve gear, but basic fishing techniques are very similar, regardless of location or fishery developmental stage.

In general, lines are hand-held and fished with the vessel either at anchor or drifting over depths of 100-500 m. Multiple hooks are generally used with baits varying, with availability, from stripped squid to tuna bellies and other fish parts. Bottom longline gear has been used in a few areas as a research and commercial gear (Lewis *et al.*, 1988; Shiota, 1987), but does not appear practical for commercial purposes.

In Hawaii the fully commercial vessels are generally 10-15 m in length with inboard diesel engines; many fishing grounds are located over 200 nmi from port, with trips lasting about 10 days. These vessels are equipped with depth sounders (mostly colour) and electronic navigational aids (e.g. Loran or satellite navigation systems) to assist in the location of suitable fishing grounds and hydraulic reels to haul fishing gear.

In addition to these large commercial vessels, Hawaii supports a small (<10 m in length) craft fleet which includes recreational and part-time fishermen in addition to a few full-time commercial fishermen. Operators of these small vessels generally fish close to port on 1-3 day trips. As with the larger vessels, most have depth sounders which are used in conjunction with land bearings to locate fishing grounds. Fishermen on these vessels typically use electric or hydraulic reels to haul lines, although a few fishermen still haul lines by the traditional hand-over-hand method.

In most other Pacific islands countries, vessels in the deep-slope demersal fishery are fewer than 10 m in length and either diesel or outboard motor powered. High technology equipment (*i.e.* depth sounders, electronic navigational systems and hydraulic or electric reels) is not common. Instead, fishing grounds are located using land bearings, and the FAO developed Samoan hand reel is in general use for gear retrieval (see Dalzell (1990) for a diagram of this reel). Trips are generally close to port and last 1-3 days.

## V. MANAGEMENT CONCERNS

Preliminary estimates of MSY and its associated level of fishing effort are important to managers. In countries with a developing fishery, governments often contribute financially to the building of a fishing fleet, as well as to shoreside support facilities such as ice houses. Foreknowledge of anticipated sustainable landings can help determine whether these expenditures are warranted. In a developed fishery, these same estimates are useful in determining when overfishing occurs. Ideally, after a fishery is developed, a time series of catch and effort data will have accumulated that would allow application of a surplus production model to the fishery, thereby refining estimates of MSY and its associated fishing effort.

Overfishing is divided into two categories. Growth overfishing occurs when fish are harvested at suboptimal size, thereby reducing overall landings. When this happens in a trawl fishery, rectification often takes the form of regulations increasing mesh size. In the deepwater demersal fisheries, however, increasing hook size does not strongly affect the size distribution of the catch (Ralston, 1982; 1990). Another corrective measure might involve establishing a minimum size limit for the catch. This is applicable to these particular fisheries only to the degree that specific sizes of fish can be targeted in the fishing operation. Unfortunately, snappers and groupers caught at the depths involved in these fisheries are landed in a moribund state due to expanded gas bladders and release of sublegal sized fish would not result in a high level of survival.

The second type of overfishing is recruitment overfishing. This occurs when the spawning stock biomass ($B_{ss}$) is reduced to such a low level that recruitment suffers. Unfortunately, spawner-recruit relationships are not known for any of the snappers and groupers. In the absence of this type of information, Beddington and Cooke (1983) suggest that $B_{ss}$ should not be reduced to lower than 20 per cent of its unexploited level. Fortunately, with knowledge of the length at maturity ($L_m$), $B_0$ and the unexploited length-frequency distribution, this biomass ratio may be monitored. Of course, direct estimates of species-specific spawner-recruit relationships are preferable and work should continue along this line.

An additional management problem arises in a multispecies fishery when some of the pertinent species are overfished and others are not. Ralston and Kawamoto (1987) report that three of the five most important species of the deep-slope fishery in the main Hawaiian Islands are overfished; of the remaining two species, one is at a near optimum level of yield and the other is underutilized. Establishing species-specific quotas may be the best management action in this case; however, effectiveness of this action would depend on the ability of fishermen to target particular species within the fishery.

Habitat enhancement is another area of concern for fishery managers. Are the deepwater snappers and groupers habitat-limited? Are there areas within their appropriate depth ranges that could be enhanced with artificial reefs? Care must be utilized before such "enhancement" is attempted. As suggested for juvenile *P. filamentosus* (Parrish, 1989; Moffitt and Parrish, *unpubl. data*), nursery habitats may be the same featureless, "unproductive" areas where habitat enhancement projects appear most promising. If buried by reef-making materials, juvenile habitat may be reduced. Also, because adults are known to aggregate around high relief structures, artificial reefs may increase catchability to such a degree that any increases in production are offset by overfishing (Moffitt *et al.*, 1989).

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# LARVAL FISH ASSEMBLAGES AND OCEANIC BOUNDARIES

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Knowledge of ichthyoplankton assemblages has its origins in the fisheries research and oceanographic expeditions of the late nineteenth century. Early ichthyoplankton studies focused on the geography and timing of spawning and the survival of the young of commercially important species, while the collections of far ranging oceanographic expeditions provided a global view of ichthyoplankton diversity and distribution patterns. The utility of ichthyoplankton approaches in fisheries research has increased in response to an increasing need for fishery-independent stock assessment, the subject of the companion symposium in this volume. With fisheries science now moving beyond single-species concepts, ichthyoplankton research has a key role in our understanding of the ecology and evolution of fish faunas and their constituent populations. The need to focus on ichthyoplankton assemblages as an integral part of their environment is central to this understanding and is the basis for this symposium.

One objective of the symposium is to review what is known about the composition and structure of larval fish assemblages in the world ocean and present the results of current research on these assemblages. The focus here is on larvae rather than total ichthyoplankton since fish eggs still are poorly known and incompletely identified in most ichthyoplankton collections. Also, many species have demersal or internally brooded eggs though their planktonic larvae are prominent members of ichthyoplankton assemblages. Taxonomic competence has advanced sufficiently over the past several decades to permit identification (at least to family) of most larvae taken in plankton survey tows (Fahay, 1983; Leis and Rennis, 1983; Leis and Trnski, 1989; Matarese et al., 1989; Miller et al., 1979; Moser et al., 1984; Jones et al., 1978, and subsequent volumes in the series; Okiyama, 1988; Olivar and Fortuño, 1991; Richards, 1985; Russell, 1976). The diversity encountered in ichthyoplankton samples places a premium on accurate identification of fish eggs and larvae. Progress in both fisheries and ecological applications of ichthyoplankton research is as dependent on advances in taxonomic competence as it is on sampling and analytical innovation.

Another central issue of the symposium is the relation of larval fish assemblages to the environment. Ichthyoplankton and associated hydrographic data accumulated over the past several decades provide a basis for addressing some fundamental questions. How are fish distributions delimited by hydrography? Does the limitation occur during early ontogeny, during the adult stage, or both? If both, what are the relative contributions of larval and adult stages? Are larval fish assemblages primarily a consequence of adult distributions or are they distinct evolutionary phenomena? Is there adaptive commonality or complementarity among component taxa of an assemblage? What can we say about the fine scale horizontal and vertical structure of assemblages and what is the relation of this structure to physico-chemical boundaries? What role do the latter play in the formation and maintenance of larval fish assemblages?

Knowledge of the physiological characteristics and energetic requirements of fish larvae is basic to the investigation of these questions. Over the past several decades, such information has accrued steadily from field and laboratory studies. Often, important advances were presented in the series of international early life history symposia which began at Lake Arrowhead, California in 1963 (Lasker, 1965). The contribution of Houde and Zastrow, the lead paper in this symposium, represents such an advance. Here, for the first time, growth, mortality, metabolic rates, stage durations, and growth and assimilation efficiencies of marine and freshwater fish larvae are summarized by ecosystem and ordinal taxonomic category. Ecosystem- and taxon-specific energy budgets derived from these calculations form the basis for an initial estimation and discussion of broad scale trophic requirements of fish larvae and lay a foundation for the papers that follow.

The papers are arranged regionally, beginning with the Central Pacific and Indo-Pacific, followed sequentially by the Antarctic, South Atlantic, western North Atlantic region, and North Pacific. Boehlert and Mundy begin this section with a survey of larval fish assemblages associated with seamounts and oceanic islands, primarily drawing from their studies in the central Pacific. They found little evidence that ichthyoplankton assemblages at seamounts differ from the background field despite the presence of physical mechanisms proposed in the literature to retain planktonic larvae at such features. This is in contrast to distinct nearshore, neritic, and oceanic assemblages described for islands. Boehlert and Mundy's discussion of mechanisms that may maintain assemblages at islands (e.g., boundary layers, small scale frontal dynamics, tidal currents, and topographically produced eddies) points to future research paths.

Some of these issues are addressed in the paper by Leis on larval fish assemblages associated with Indo-Pacific coral reefs. An important finding was that larval fish assemblages associated with coral reefs have distinct spatial structure that varies vertically and horizontally. Vertical patterns result from larval behavior and break down at night. Horizontal patterns are dependent on habitat and topography with most variation in the on/offshore dimension. Leis found that the decline in abundance of shorefish larvae with increasing distance from the reef varied markedly among taxa. This points to the importance of larval behavior in determining assemblage composition and structure, as does the fact that habitat changes, particularly those in close proximity to the reef, can result in striking changes in assemblages.

The paper by Kingsford further emphasizes the potential role of behavior of early life-history stages and environmental structure as a determinant of assemblage pattern. The recent work of the author and others suggests that the spatial scale of abiotic and biotic structures in the pelagic environment may range more than a thousandfold and that survival of larval and juvenile fishes of a wide array of taxa may depend on associations with these structures. Moreover, the effect of these structures may be accentuated by their accumulation at fronts. The author documents potential associations of 72 fish families with large pelagic structures (drift algae, gelatinous zooplankton, flotsam) and discusses the role that small scale structure (e.g., cell aggregations, marine snow) may play in modifying the trophic environment and affecting survival of fish larvae.

In our view, future investigations of the role of structure in the pelagic environment and its relation to the early stages of fishes must ultimately address the more general subject of zooplankton contagion and the adaptations that larval fish have evolved to find and exploit food patches resulting from contagious distribution. These structures, essentially invisible to net sampling, must play a key role in early survival since integrated measures of larval fish prey from net samples indicate that average concentrations are typically below the minimum threshold for first-feeding larval fishes.

The summary of Antarctic larval fish assemblages by Loeb, Kellerman, North, White, and Koubbi is comprehensive and timely. The endemic and specialized Antarctic fauna is highly vulnerable to exploitation and habitat degradation and many species have experienced dramatic declines over the recent past. The shorefish fauna is dominated by demersal or benthopelagic notothenioids whose early life histories are characterized by large egg size, morphologically advanced hatchlings, and an extended pelagic pre-settlement phase. Bounded by the Antarctic Polar Front, the Southern Ocean is a habitat dominated by strong currents and gyres, complex topography (basins, ridges, islands, and ice shelves), and a highly seasonal production cycle that is closely linked with a distinct seasonal hatching sequence for components of the ichthyofauna. Initial analyses of Antarctic and Sub-Antarctic larval fish assemblages indicate a finely tuned and highly integrated system reflective of a unique evolutionary history and a complex and demanding environment.

Olivar and Shelton describe the larval fish assemblages of the Benguela Current region of South Africa and Namibia. Like other eastern boundary current systems, it is driven by a cold subpolar current, experiences strong coastal upwelling and high seasonal productivity, and is a region of striking oceanographic complexity where vastly different fish faunas merge at water mass boundaries. Another feature shared with other eastern boundary regions is a highly productive fishery dominated by resident species (or populations) of *Sardinops, Engraulis, Trachurus,* and *Merluccius.* Variations in the upwelling regime strongly affect (and may control) assemblage composition and the abundance of component taxa.

The papers on the western North Atlantic region describe the composition and dynamics of larval fish assemblages on a wide range of scales. The paper by Richards, McGowan, Leming, Lamkin, and Kelley provides a fine scale view of assemblages across regions of the Loop Current, the dominant hydrographic feature of the Gulf of Mexico. The assemblages are strikingly diverse, reflective of extensive tropical oceanic and mesopelagic elements augmented by a highly diverse tropical shelf fauna at the Loop Current front. Principal components analysis revealed distinct assemblages on the oceanic and shelf sides of the front and demonstrated the role of the front in delimiting assemblage boundaries. Although no distinct frontal assemblage was apparent, larvae of scombrids and carangids were closely associated with the front (usually the oceanic side) and frontal mixing and dynamics may be important in their distribution and survival.

Govoni describes the distributions of larva assemblage indicator species at the Mississippi River plume front and Gulf Stream front off the South Atlantic Bight (SAB) in relation to hydrographic features, and postulates physical mechanisms that may result in flux of larvae across fronts. The early life histories of gulf and Atlantic menhaden (*Brevoortia patronus, B. tyrannus*) and spot (*Leiostomus xanthurus*) are closely tied to these frontal regions. Their larvae are concentrated in these regions by entrainment through frontal convergence and possibly by migration and selective spawning behavior of the adults. Presumably elevated productivity associated with frontal dynamics (e.g., upwelling, shear) provides a propitious trophic environment, while larvae are confined within the appropriate water mass by frontal boundaries. Shelf-break fronts contribute to the complexity of both of these frontal systems. Displacement of larger larvae to nursery areas requires flux across frontal boundaries and the author explores the potential means by which advection may occur. Dynamic processes (e.g., filament, eddy, meander formation) in conjunction with specific behavior patterns may be involved in translocation of larvae, although evidence for these or other mechanisms has yet to be revealed.

The processes are further addressed by Cowen, Hare, and Fahey in relation to larval fish assemblages of the New York Bight. They described five distinct assemblages whose membership and boundaries varied over the summer. Assemblages of the New York Bight and the Middle Atlantic Bight (MAB) are a mixture of year-round resident species and species from the south, derived either from northward migration of spawners or from larvae advected northward from the SAB. The authors propose that larvae spawned in the SAB and entrained along the inner boundary of the Gulf Stream may be translocated shoreward by a combination of dynamic processes (e.g., warm-core rings spun off the Gulf Stream, mesoscale eddies associated with the shelf/slope front, sub-surface intrusions of slope water associated with the pycnocline). They present evidence that stage-specific behavior may play an important part in shoreward movement of larvae. Some species migrate downward to the zone of cross-shelf intrusion and others may actively migrate shoreward after reaching an advanced larval stage.

Doyle, Morse, and Kendall describe and compare the larval fish assemblages off the northeastern and northwestern coasts of the U.S.A. in an effort to identify mechanisms involved in the evolution of these assemblages. Description of the east coast assemblages is based on MARMAP, a comprehensive fishery ecosystem study that occupied nearly 11,000 ichthyoplankton/oceanographic stations between Cape Hatteras and Nova Scotia from 1977 to 1987. West coast assemblages are described from a series of 10 ichthyoplankton surveys conducted off the coasts of Washington, Oregon, and Northern California from 1980 to 1987. Georges Bank and the Gulf of Maine have distinct assemblages that are contained within semi-isolated circulation systems. Shelf and Slope/Oceanic assemblages of the MAB result from interaction between seasonal cycles (temperature, production, and spawning) and the complex MAB recirculation system. In contrast, assemblages off the west coast have evolved in relation to two dominant environmental features, the California Current and its associated seasonal upwelling cycle. Spawning of taxa that contribute to shelf and slope assemblages appears to be correlated more closely with the onshore/offshore shift in Ekman transport than with production cycles.

Moser and Smith described the larval fish assemblages of the California Current region based on the 30-year time series of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and show how vertical and horizontal distributions of component taxa change across a front. Three major assemblages (Northern Complex, Southern Complex, and Southern Coastal Complex) are apparent from analyses based on occurrence and abundance of larvae. Groups within the Northern and Southern Complexes are closely associated with the distinct water masses of the region (Subarctic, Transitional, Eastern Tropical Pacific, Central). The CalCOFI station grid is adequate to define assemblage distributions; however, identification of variables that may be important in delimiting assemblage boundaries requires fine scale horizontal and vertical sampling. Moser and Smith report the results of a cruise conducted off Ensenada, Mexico, where a semi-permanent front separates cold eutrophic water to the north from warm oligotrophic water to the south. The study demonstrated the transition from Subarctic-Transitional to Eastern Tropical Pacific fauna and showed a marked change in vertical distributions for taxa occurring on both sides of the front. The authors suggest that this shift in vertical distribution may be related to trophic conditions and larval feeding behavior, factors which also may play key roles in the evolution of larval fish assemblages.

McGowen's study on nearshore larval fish assemblages of the Southern California Bight (SCB) identified six assemblages that were related to seasonality and cross-shelf distribution. The major assemblages were a winter-spring shelf, a summer shelf, and an offshore assemblage that was similar to the principal assemblage of Moser and Smith's Northern Complex. Longshore variation in assemblage structure was not evident in the SCB; however, there was some evidence that semi-isolated habitats off rocky headlands may have assemblages that are distinct from those of the open coast. Life-history strategies of SCB taxa are characterized by mechanisms which retain larvae near shore; however, recruitment of some populations of shorefish taxa larvae are dependent on larvae entering the SCB gyre (Southern California Eddy).

These symposium contributions have accomplished the primary goal of bringing together and summarizing what is known about larval fish assemblages. The 12 papers reveal a large and growing information base for most regions of the world ocean and indicate that we can begin to address some fundamental questions pertaining to larval fish assemblages. The basis for the taxonomic composition of larval fish assemblages is one such issue and it is clear that adult distributions and spawning seasonality are principal causal factors. It is also apparent that these are not the only causal factors since most assemblages include taxa that are geographically and/or temporally separated from adult spawners. Just as the basis for assemblages is heterogeneous, so is spatial distribution among assemblage members. Our appreciation of fine scale horizontal and vertical pattern within assemblages has grown considerably with the advent of discrete multiple samplers; however, this field of study is just beginning and it is obvious that much more emphasis must be placed here if we are to progress in our understanding of assemblage dynamics.

The taxa that make up these assemblages of larvae are characterized by a great diversity of size, stage duration, morphology, and pigmentation. A reasonable assumption is that these reflect: 1) an equally great diversity of adaptations for survival in the planktonic environment and 2) on a larger scale, a diverse constellation of successful early life-history strategies. In contrast, Houde and Zastrow show a general homogeneity in temperature-adjusted rates for growth, ingestion, mortalilty, and metabolism across broad taxonomic categories and ecosystems. Moreover, these authors indicate that the most striking difference found in their survey—the lower metabolic and mortality rates of freshwater larvae—can be ascribed to greater weight at hatching compared with marine larvae. We suggest that these findings and those of other symposium contributors point to the importance of behavior in concert with morphological and pigment specializations as prime factors in adaptation and survival of larvae.

We can hope that information on rates and energetics of the great mesopelagic and oceanic larval fish assemblages can be added to that amassed and synthesized by Houde and Zastrow. Likewise, we must increase our knowledge of vital rates and processes of later life-history stages. Ichthyoplankton surveys have been used widely to estimate fish biomass because they are a comprehensive and relatively inexpensive fishery-independent method. The accuracy and precision of these estimates depends on the competency of the plankton work and on the state of knowledge of the reproductive biology and demography of the subject populations. Reproductive and demographic information is scanty for all but a few fish species and this precludes the application of ichthyoplankton methods to multi-species fishery management problems, as well as to ecological and community research. For some species, such as the northern anchovy (*Engraulis mordax*) and the herring (*Clupea harengus*), we can estimate fairly accurately the juvenile and adult biomass represented by a planktonic egg or larva (Lasker, 1985; Heath, this volume). Much research effort is needed if we are to extend this competence beyond a few high profile coastal species. We are just beginning to appreciate the diversity of reproductive and demographic patterns of mesopelagic (e.g., Childress et al., 1980; Gjøsaeter and Kawaguchi, 1980; Miya and Nemoto, 1991) and oceanic fishes (e.g., Davis et al., 1991; Jenkins et al., 1991; Richards, 1991). Small additions to our knowledge of reproduction and demography of these faunas will immediately increase the usefulness of ichthyoplankton surveys and set us on the road toward multispecies and ecosystem studies.

The relation of larval fish assemblages to hydrography was treated extensively in this symposium and it is clear that fronts and other dynamic features as well as water-mass properties play important roles in the regulation of assemblages and, ultimately, in the regulation of parent fish populations. Just as was suggested for the study of pattern within assemblages, advances in our knowledge of assemblages at their boundaries will require fine scale, three-dimensional collection of fish larvae and the principal elements of their biotic and abiotic environment. Many of the contributions indicated strong interplay between frontal features and larvae of coastal fish populations. Frontal systems, especially those that include currents, are characterized by elevated productivity and by an array of dynamic features with potential for advection and translocation of early life-history stages. The role of such systems in the generation of assemblages may be as important as their role in maintaining assemblage boundaries.

A final consideration is whether larval fish assemblages have an intrinsic adaptive function as has been suggested by Frank and Leggett (1983). Are larval fish assemblages, each derived from highly diverse phylogenetic lineages and adult habitats, anything more than the result of convergent evolution of life-history strategies? Detection of an intrinsic adaptive function for these assemblages is daunting, given our limited understanding of structure and process in pelagic communities, in general. Multispecies approaches to the study of fish populations are just emerging, as are comprehensive studies of plankton communities; larval fish assemblages are subsets of these. Doyle et al. (this volume) note McGowan and Miller's (1980) emphasis on the relative rarity of fish larvae compared with other plankters and aptly suggest that, "It may be necessary to focus on the zooplankton assemblage in its entirety . . . to understand fully the multispecies spatial patterns that prevail among larval fishes." Extending this further, we suggest that it is necessary to consider the abundance of later ontogenetic stages of species that make up a larval fish assemblage. The impact of planktivorous juveniles and adults of the major larval fish groups (coastal pelagic, oceanic, and mesopelagic species) on the biomass and species structure of zooplankton populations may be far greater than what can be inferred from numerical dominance of major crustacean groups over larval fishes. The point is that population regulation may occur over all scales and ontogenetic stages and one could not expect to gain insight into the dynamics of larval fish assemblages without making progress in understanding the systems in which they are embedded. In this context larval fish assemblages may be opportune windows into the communities to which they contribute.

## Acknowledgments

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# LARVAL FISH ASSEMBLAGES OF THE CALIFORNIA CURRENT REGION AND THEIR HORIZONTAL AND VERTICAL DISTRIBUTIONS ACROSS A FRONT

*H. Geoffrey Moser and Paul E. Smith*

## ABSTRACT

Cruises of the California Cooperative Oceanic Fisheries Investigations occupied 31,214 survey stations in a one million km$^2$ area off California and Baja California during 1951 to 1984. Recurrent group analysis of 249 larval fish taxa placed 36 taxa in 12 recurrent groups. These groups reflect the oceanographic complexity of the region with Subarctic-Transitional, Eastern Tropical Pacific (ETP), and Central Water Mass components. The major shorefish recurrent group is associated with the large shelf area of Sebastian Viscaino Bay off central Baja California. Cluster analysis using correlation coefficients of abundance as the measure of distance and principal component analysis produced groupings that agreed in general with groups formed by presence-absence analysis. Environmental effects on these groups were studied by examining changes in horizontal and vertical distribution across a frontal region. Plankton samples from the FRONTS 85 cruise conducted in July, 1985, southwest of the Southern California Bight, allowed us to investigate the fine scale distribution of assemblages across a semi-permanent frontal zone separating cold eutrophic water to the north from relatively warm, oligotrophic water to the south. Ichthyoplankton samples from a 120-n. mi. transect across the front, including 42 oblique bongo tows and 8 MOCNESS tows to 1,000 m, demonstrated: 1) the transition between Subarctic-Transitional and ETP/Central Water Mass species, and 2) distinctly different patterns of vertical distribution for the same species at the north and south sides of the front.

Research on larval fish assemblages has increased over the past several decades in concert with increasing interest in plankton ecology and dynamics. Ichthyoplankton surveys have produced a growing fund of information on assemblages from major ocean regions [e.g., Eastern Atlantic—Doyle and Ryan (1989), Olivar (1990), Sabatés (1990); Western Atlantic—de Ciechomski et al. (1991), Ditty et al. (1988), Morse et al. (1987), Richards (1984), Richards et al. (1989); Eastern Pacific—Ahlstrom (1972a), Kendall and Clark (1982), Kendall and Dunn (1985), Leis and Miller (1976), Loeb (1980), Loeb and Rojas (1988), Richardson et al. (1980), Santander and Flores (1983), Savage (1989); Western Pacific—Leis and Goldman (1987), Young et al. (1986); Indian Ocean—Nellen (1973); Antarctic—Kellerman and Kock (1988)].

Ichthyoplankton studies in the California Current region were initiated in response to the collapse of the Pacific sardine, *Sardinops sagax,* over a 22-year period from about 1925 to 1947. In 1949 the California Cooperative Oceanic Fisheries Investigations (CalCOFI) began conducting annual biological/oceanographic surveys over a >1 million km$^2$ grid extending from northern California to Cape San Lucas, Baja California (Fig. 1). The fact that the CalCOFI sampling grid overlays three coastal zoogeographic provinces, a coastal upwelling zone, and three oceanic water masses has allowed us to examine structure and variation in adjacent ichthyoplankton assemblages for portions of the CalCOFI time series (Loeb et al., 1983; Moser et al., 1987) and for the entire time series in this paper.

An extensive oceanographic literature exists for the California Current region (Reid, 1988) and considerable attention has been directed to the fronts that separate the major water masses (Lynn, 1986). The development of satellite remote sensors and other technological advances has resulted in much recent interest in fine scale oceanographic features (Simpson et al., 1984; Haury, 1984; Pelaez and

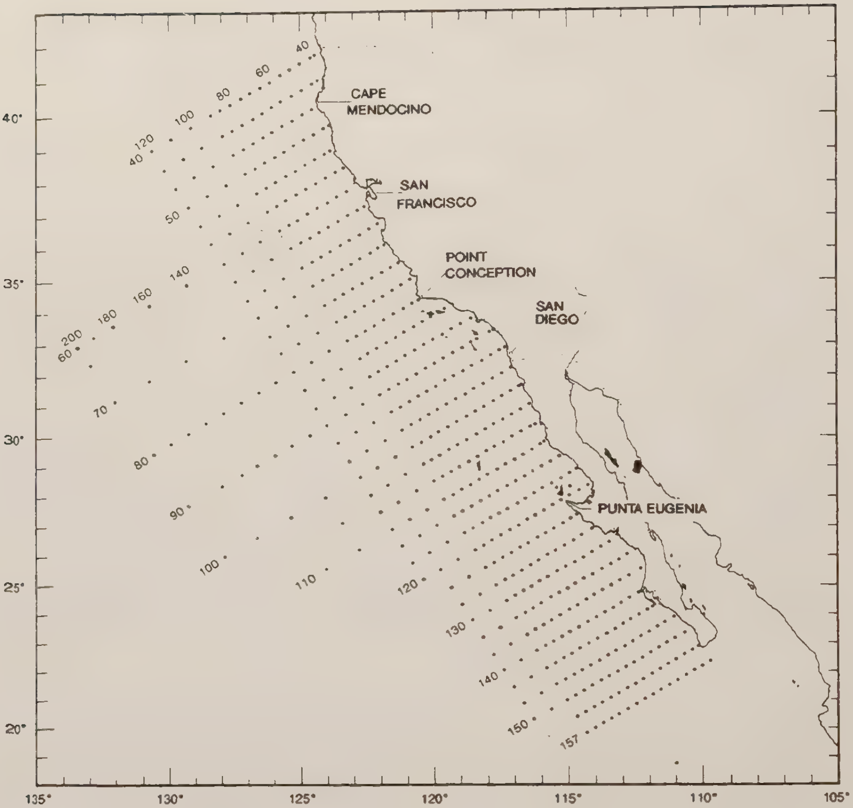

Figure 1. Station pattern for California Cooperative Oceanic Fisheries Investigations survey area. Numbers on the left of the pattern are CalCOFI survey line numbers; numbers above the pattern are station numbers.

McGowan, 1986; Lynn and Simpson, 1987; Niiler et al., 1989; Strub et al., 1991). Of particular interest is the frontal structure formed where the California Current flows shoreward at about 32°N, separating relatively cold, fresh, eutrophic water to the north from warmer, oligotrophic, more saline water to the south. Haury et al. (1993) refer to this semi-permanent feature as the Ensenada Front. The physical, chemical, and biological properties of this front were sampled intensively on the FRONTS 85 cruise (Niiler et al., 1989; Haury et al., 1986). Ichthyoplankton samples from this cruise are the basis for our study of the horizontal and vertical distribution of larval fish assemblages across the front in relation to the abiotic and biotic environment.

We describe the composition and structure of the CalCOFI ichthyoplankton assemblages from recurrent group analysis of the entire 40-year time series. These assemblages are compared with groupings from analyses based on taxon abundance using clustering and ordination techniques. We use presence-absence and abundance analyses to define assemblages because data on taxa "are often very far from being randomly and normally distributed and linearly correlated" (Hubalek, 1982). Results of theoretical work on alternative assembly methods (Hubalek, 1982) and empirical testing (MacDonald, 1975; Hubalek, 1982; Magurran,

1988) generally support Fager and McGowan's (1963) proposal that, for extensive surveys covering several habitats, it is preferable to use presence-absence techniques where joint absences are disregarded. Recurrent group techniques are particularly useful when attempting to describe the interaction of groups of species in which competition or predation, for example, could influence the very quantities used in describing the interaction (Fager, 1957).

Following our summarization of the assemblages, we describe the fine scale vertical and horizontal distribution of certain assemblage groups along a transect across the Ensenada Front. Our purpose is to determine whether assemblage distributions are affected by the abrupt hydrographic changes associated with the front. Specifically, do incidence and abundance of taxa change along the transect and are their vertical distributions different at the north and south ends of the transect on each side of the front? Are shifts in distribution and abundance of taxa across the front coherent within assemblages? Do assemblages differ in the way they react to the front? Can these distributional shifts be linked to specific environmental factors? If so, do these linkages suggest causal factors that may delimit larval fish distributions and form the bases for assemblages? Finally, we examine the fine scale horizontal and vertical distributions of larval fish taxa and assemblages from the FRONTS 85 cruise in relation to the CalCOFI time series and discuss how this new information may affect interpretation of the CalCOFI data.

## METHODS AND MATERIALS

*CalCOFI.*—The description of larval fish assemblages in the CalCOFI region is based on 31,214 plankton-net tows taken on CalCOFI surveys from 1951 to 1984; these tows yielded circa 12.4 million fish larvae distributed in 249 taxa. The overall survey area extended from the Oregon-California border to the southern tip of Baja California, Mexico and offshore to 280 to 360 n. mi. However, most annual surveys covered a smaller area from San Francisco, California to San Jaunico Bay, Baja California and seaward to 160 to 250 n. mi. (Fig. 1). The survey lines, arranged perpendicular to the coastline, are 40 n. mi. apart and principal stations are placed at 40-n.-mi. intervals on the lines. Usually stations were occupied at 20-n.-mi. intervals on the inner half of the pattern and at closer intervals near the coast and islands to accommodate these features. Surveys were made each year from 1951 to 1969, and thereafter every third year until 1984. The sampling pattern was occupied monthly from 1951 to 1960, quarterly from 1961 to 1965, and on a monthly basis from 1966 to 1984. During 1972–1984 there were six or seven monthly cruises per year.

At each station a double oblique plankton-net tow was made to a standard depth (to 140 m during 1951 to 1968 and to 210 m thereafter). Details of CalCOFI sampling methods and laboratory procedures are described in Smith (1971), Kramer et al. (1972), and in a series of 24 data reports that lists the ichthyoplankton and associated station data for each CalCOFI survey conducted from 1951 to 1984 (Ambrose et al., 1987; Stevens et al., 1990).

For presence-absence analysis of the assemblages we employed Fager's (1957) recurrent group technique, as in an earlier study of a portion of the data base (Moser et al., 1987). All 249 taxa identified from the net tows taken on CalCOFI surveys during 1951 to 1984 were used in this analysis. An affinity index was calculated for each pair of taxa that ever co-occurred in a plankton sample. From these indices recurrent groups of taxa were formed by the REGROUP program using a minimum index value of 0.3. Taxa were recognized as group "associates" when they had significant affinity indices ($\geq 0.3$) with one or more but not all group members in one or more groups. A group "affiliate" had its highest affinity index (always $<0.3$) with a particular group. Each recurrent group was given a name based on a prominent member taxon as in Moser et al. (1987).

Analyses using larval fish abundance were performed on the 25 most abundant taxa from 1954 to 1960 in the region of most consistent spatio-temporal coverage extending from CalCOFI line 80 (Point Conception, California) to line 127 (just south of Point Eugenia, Baja California) and seaward to station 90 on each line (200 to 300 n. mi. offshore). The area was divided into rectangular sub-areas (Smith, 1971), each typically 40 × 120 n. mi. representing an area of circa 4,800 n. mi.$^2$. Standardized counts of taxa were pooled by month for each sub-area for the years 1954 to 1960 and transformed by the formula, $\log(10 \cdot x + 1)$, where x is taxon abundance (number of larvae per 10 m$^2$ surface area). Linear correlation coefficients were computed and expressed as "distance" (distance = 1 − correlation coefficient). At each step, the distance was computed between all possible pairs of taxa and the two taxa with the shortest distance between them were classified into one cluster. After defining a cluster, a centroid linkage algorithm was used to form a new centroid (pseudo-taxon) by taking the average of the abundance of taxa within the cluster. The distances and linkage procedures were then summarized in a dendrogram (Kendall et al., 1983; Dixon, 1988). The logarithm-transformed data were also used to compute principal components; in this analysis a set of principal components was extracted from a variance-covariance matrix of the data set and the coefficients of the first and second principal components associated with each species were plotted on X-Y coordinates, as a means of summarizing variation in abundance of component taxa (Morrison, 1990).

*FRONTS 85 Cruise.*—Data on fine scale vertical and horizontal distribution of larval fishes were obtained from samples taken on Leg II of the FRONTS 85 cruise conducted by Scripps Institution of Oceanography aboard the R/V NEW HORIZON, July 1 to 23, 1985, southwest of the Southern California Bight, in an area characterized by a semi-permanent frontal zone (Haury et al., 1986, 1993). Leg I (July 1 to 11) was an intensive physical oceanographic survey of the frontal structure detected by AVHRR satellite images (Niiler et al., 1989) and Leg II (July 12 to 23) was a biological/oceanographic survey that occupied 37 stations on a south-north and a west-east transect crossing the front (Fig. 2). Stations on the west-east transect had single bongo tows and are not included in this paper. The south-north transect was 120 n. mi. in length, consisted of nine station sites (Stations 2 to 10, Fig. 2), each occupied three times on sequential traverses during July 13 to 21. Stations were circa 13 n. mi. apart, except the terminal stations were 20 n. mi. from their neighboring station. A total of 42 oblique plankton-net tows to 210 m depth was taken on the transect using a 71-cm paired bongo net with 0.505-mm mesh. At each terminal station, two day/night pairs of discrete, vertically stratified tows were made at 2-d intervals with a MOCNESS 1-D (1-m$^2$ mouth opening) equipped with 0.333-mm mesh nets (Wiebe et al., 1985). Sequential samples were taken at the following 16 depth strata on each tow: 1,000–850 m; 850–700 m; 700–550 m; 550–400 m; 400–300 m; 300–250 m; 250–225 m; 225–200 m; 200–175 m; 175–150 m; 150–125 m; 125–100 m; 100–75 m; 75–50 m; 50–25 m; 25–0 m.

Hydrographic casts to a maximum depth of 1,000 m, made at each station, consisted of 20 Nansen bottles from which temperature, salinity, oxygen, and nutrients were determined from all depths sampled. A total of eight primary productivity casts was made on the south-north transect. Light penetration was estimated by Secchi depth and by an irradiance meter. Examples of these data, collected in association with productivity measurements, are presented to provide a general comparison of light penetration on each side of the front. Plankton biomass for each sample was determined in the laboratory by measuring the wet displacement volume after removal of large (>5 ml) organisms (Haury et al., 1986, 1993).

Fish eggs and larvae were sorted from the samples at the NMFS Laboratory, La Jolla, California, and identified to the lowest taxon possible. Counts of larvae from the bongo net tows were multiplied by a standard haul factor (Smith and Richardson, 1977) and expressed as number per 10 m$^2$ of sea surface. Counts from the MOCNESS tows were expressed as number per 1,000 m$^3$ of water filtered.

Environmental parameters associated with the vertical distributions of larval fish taxa from the MOCNESS samples were evaluated by calculating larva-weighted means for each parameter. Values for temperature, salinity, density (sigma-theta), dissolved oxygen, nitrate, and chlorophyll-*a* were obtained from Nansen bottle casts associated with each MOCNESS cast. Parameters were estimated by linear interpolation of values at "standard" depths (Haury et al., 1986) when they did not coincide with strata sampled by the plankton nets. Larva-weighted mean environmental parameters ($\overline{st}$) were calculated using the formula:

$$\overline{st} = \sum f_i v_i st_i \Big/ \sum f_i v_i$$

where: $f_i$ is the number of fish larvae of taxon *i* from a net sample; $v_i$ is 1,000 divided by the actual volume of water filtered estimated for each depth stratum for each tow; and, $st_i$ is the mean of the interpolated environmental values for the nominal depth at opening and closing of each net.

## RESULTS

### CalCOFI Time Series

*Recurrent Groups.*—The number of taxa per standard CalCOFI tow ranged from 0 to 29 with a mode of six taxa per tow (Fig. 3). Recurrent group analysis of the pooled 1951–1984 data set placed 32 taxa in 10 groups that were connected directly or indirectly with each other or through ties with five associate taxa (Fig. 4,

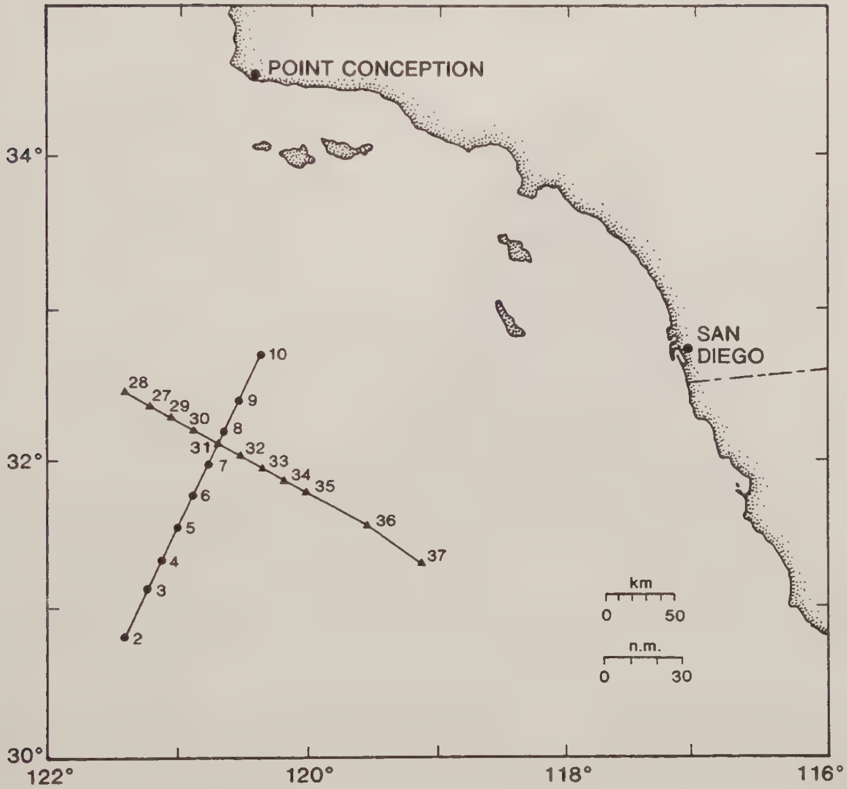

Figure 2. Stations occupied by RV New Horizon on Leg II of the FRONTS 85 cruise, 12 to 23 July, 1985. Modified from Haury et al. (1986).

Appendix). Within this network, intergroup affinities formed two large complexes: 1) a Northern Complex consisting of a five-member group (LEUROGLOSSUS) and four taxon pairs (TARLETONBEANIA, PARALICHTHYS, SARDINOPS, CITHARICHTHYS) and 2) a Southern Complex consisting of a six-member group (SYMBOLOPHORUS), a four-member group (VINCIGUERRIA), and two taxon pairs (CERATOSCOPELUS, TRIPHOTURUS). One group of five shorefish taxa (SYNODUS) formed no inter-group connections but had three associate taxa; we refer to this recurrent group and its associates as the Southern Shelf Complex. Five pairs of taxa formed isolated groups with no connections to other groups or associate taxa (Appendix). Two of these pairs were based on multiple co-occurrences (*Citharichthys fragilis-Citharichthys xanthostigma, Cubiceps pauciradiatus-Psenes sio*) and three were based on single co-occurrences (Balistidae-Fistulariidae, *Cyclopsetta* spp.-Microdesmidae, *Chaetodipterus zonatus*-Sparidae).

Northern Complex. The LEUROGLOSSUS group, consisting of five taxa, is the largest group in the Northern Complex (Fig. 4, Table 1). Group members have primarily subarctic-transitional associations with highest abundances in winter to spring. Incidence and abundance are high in coastal regions for all taxa, particularly *Merluccius productus, Sebastes* spp., and *Leuroglossus stilbius*. The

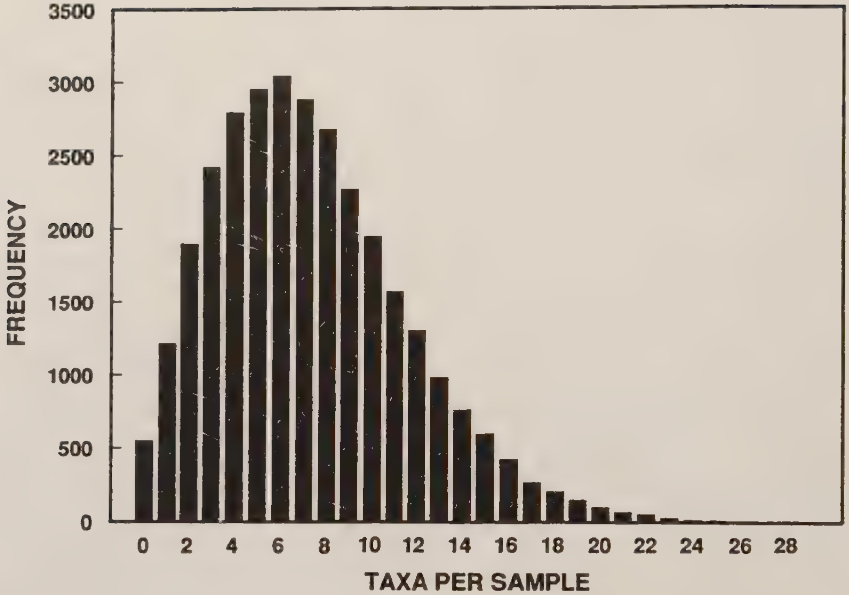

Figure 3. Numbers of larval fish taxa per sample in 31,214 CalCOFI tows taken during 1951 to 1984.

distribution of larvae for the latter is centered in the Southern California Bight. *Bathylagus ochotensis* and *Stenobrachius leucopsarus* have more northerly distributions than other group members and extend farther offshore than the others (Ahlstrom, 1972b).

TARLETONBEANIA (Fig. 4, Table 1) is composed of two subarctic-transitional species with summer maxima in abundance (Moser and Ahlstrom, 1970; Ahlstrom et al., 1976). *Tarletonbeania crenularis* has significant affinities with all but *M. productus* in the LEUROGLOSSUS group and *Icichthys lockingtoni* has significant affinities with *B. ochotensis* and *S. leucopsarus,* the more offshore members of the LEUROGLOSSUS group.

CITHARICHTHYS is composed of an abundant coastal pelagic species, *Engraulis mordax,* and the flatfish genus *Citharichthys.* The genus *Citharichthys* is represented principally by four species in the CalCOFI area. These species have broadly overlapping ranges; however, *C. sordidus* and *C. stigmaeus* have more northerly distributions than *C. fragilis* and *C. xanthostigma* whose ranges are centered off Baja California (Ahlstrom and Moser, 1975; original data). Since larvae of *Citharichthys* were identified to species only during the years 1954 to 1960, the relationships of the component taxa are obscured in the pooled 1951–1984 data. *Engraulis mordax* had significant affinities with all members of the LEUROGLOSSUS group except *B. ochotensis. Citharichthys* spp. and *Sebastes* spp. shared a significant affinity index, while *C. fragilis* and *C. xanthostigma* formed a recurrent group with no significant affinities to other groups (Fig. 4, Table 1, Appendix).

CITHARICHTHYS is linked with two other groups in the Northern Complex, each formed by taxon pairs: SARDINOPS, consisting of the coastal pelagics *Sardinops sagax* and *Scomber japonicus*; and PARALICHTHYS, formed by the

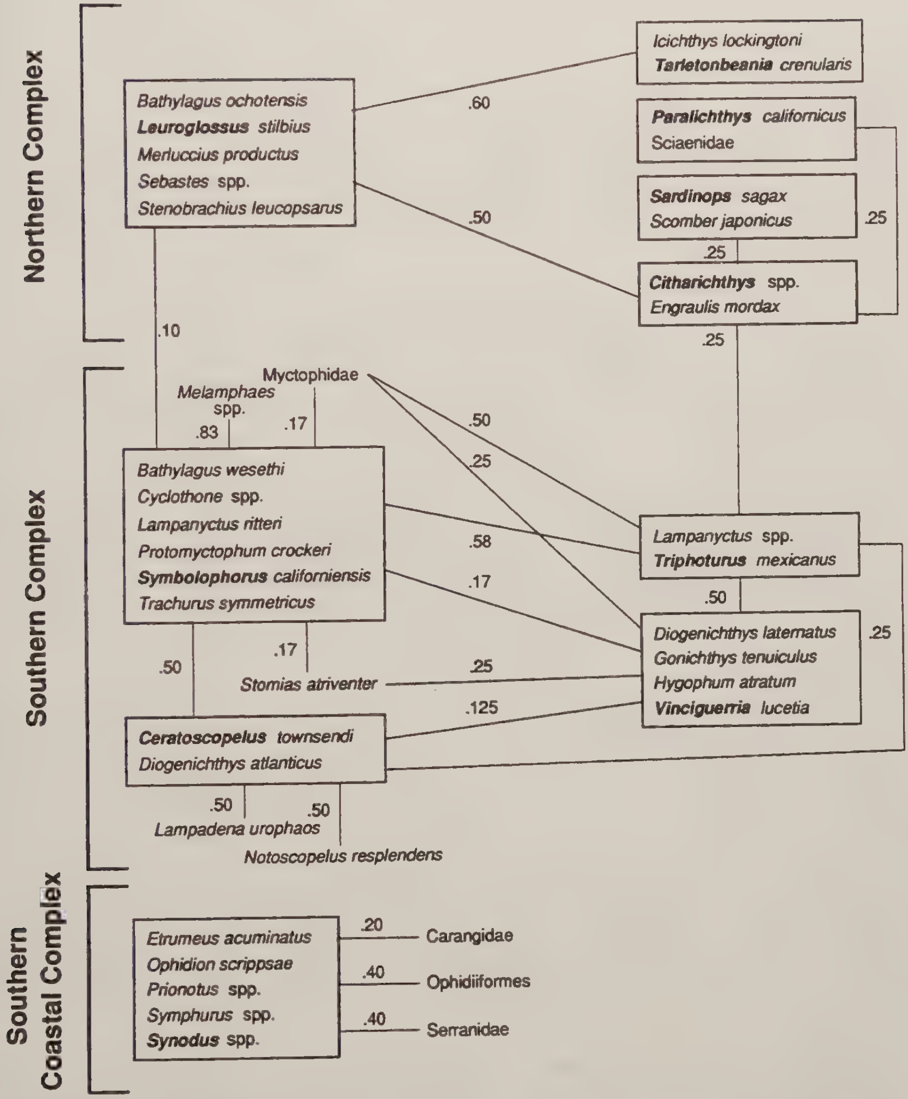
Northern Complex
Icichthys lockingtoni
Tarletonbeania crenularis
Bathylagus ochotensis
Leuroglossus stilbius
Merluccius productus
Sebastes spp.
Stenobrachius leucopsarus
.60
Paralichthys californicus
Sciaenidae
Sardinops sagax
Scomber japonicus
.50
.25
.25
Citharichthys spp.
Engraulis mordax
.10
.25
Southern Complex
Myctophidae
Melamphaes spp.
.83
.17
.50
.25
Bathylagus wesethi
Cyclothone spp.
Lampanyctus ritteri
Protomyctophum crockeri
Symbolophorus californiensis
Trachurus symmetricus
.58
.17
Lampanyctus spp.
Triphoturus mexicanus
.50
.17
.50
Stomias atriventer
.25
.125
Diogenichthys laternatus
Gonichthys tenuiculus
Hygophum atratum
Vinciguerria lucetia
.25
Ceratoscopelus townsendi
Diogenichthys atlanticus
.50
.50
Lampadena urophaos
Notoscopelus resplendens
Southern Coastal Complex
Etrumeus acuminatus
Ophidion scrippsae
Prionotus spp.
Symphurus spp.
Synodus spp.
.20
Carangidae
.40
Ophidiiformes
.40
Serranidae

Figure 4. Composition and interrelationships of recurrent groups of larval fishes (in boxes) and their associates (not enclosed) in the CalCOFI area, 1951 to 1984, from an analysis of 31,214 samples. A line connecting recurrent groups to other recurrent groups or to associate taxa indicates there are intergroup pairs with significant affinity indices (≥0.3). The value associated with each line represents the number of significant intergroup affinity pairs divided by the total possible pairs. The name for each recurrent group (e.g., LEUROGLOSSUS) is based on the generic name indicated in bold letters.

flatfish *Paralichthys californicus* and the demersal shorefish family Sciaenidae (Fig. 4, Table 1). SARDINOPS is linked with CITHARICHTHYS through a significant affinity index between *S. sagax* and *E. mordax*. Both members of the SARDINOPS group are characterized by dynamic fluctuations in population size

Table 1. Taxonomic composition of recurrent groups of larval fishes in CalCOFI surveys from 1951 to 1984, number of occurrences and months of high abundance (peak month in parentheses), and zoogeographic and depth distribution of adults. Information on the distribution of adult fishes summarized from Brodeur (1988), Eschmeyer et al. (1983), Matarese et al. (1989), Matsuda et al. (1984), Miller and Lea (1972), Moser et al. (1987), Willis et al. (1988), Wisner (1976), and original data (CP = coastal pelagic, D = demersal, EP = epipelagic, ETP = eastern tropical Pacific, MEP = migrates to epipelagic, MP = mesopelagic, NT = no trend, S-T = subarctic-transitional, SbT = subtropical, T = transitional, Tr = tropical, WWC = warm water cosmopolite)

| Recurrent group | Family | Occurrence | Peak abundance | Distribution | Adult habitat |
|---|---|---|---|---|---|
| Northern Complex | | | | | |
| LEUROGLOSSUS group | | | | | |
| *Bathylagus ochotensis* | Bathylagidae | 4,555 | Jan–Mar (Mar) | S-T | MP (49–901 m) |
| *Leuroglossus stilbius* | Bathylagidae | 8,509 | Jan–Apr (Mar) | T | MP (to 690 m) |
| *Merluccius productus* | Merlucciidae | 7,372 | Jan–Mar (Feb) | S-T | D (to 914 m) |
| *Sebastes* spp. | Scorpaenidae | 12,322 | Jan–Apr (Jan) | S-T, T | D (to 732 m) |
| *Stenobrachius leucopsarus* | Myctophidae | 7,258 | Jan–Apr (Mar) | S-T | MP (MEP) |
| TARLETONBEANIA group | | | | | |
| *Icichthys lockingtoni* | Stromateidae | 1,992 | Jun–Jul (Jun) | S-T | EP (to 91+ m) |
| *Tarletonbeania crenularis* | Myctophidae | 4,041 | NT (Jun) | S-T | MP (MEP) |
| CITHARICHTHYS group | | | | | |
| *Citharichthys* spp. | Paralichthyidae | 6,322 | Jun–Oct (Aug) | S-T to Tr | D (to 549 m) |
| *Engraulis mordax* | Engraulidae | 14,486 | Jan–Apr (Mar) | T | CP (to 210 m) |
| PARALICHTHYS group | | | | | |
| *Paralichthys californicus* | Paralichthyidae | 1,105 | Feb–Mar (Feb)<br>Jul–Aug (Aug) | T to SbT | D (to 183 m) |
| Sciaenidae | Sciaenidae | 1,973 | Dec–Mar (Jan)<br>Jul–Aug (Aug) | T to Tr | D (to 183 m) |
| SARDINOPS group | | | | | |
| *Sardinops sagax* | Clupeidae | 2,999 | Feb–Sep (Aug) | T | CP |
| *Scomber japonicus* | Scombridae | 1,211 | May–Aug (Aug) | T to SbT | CP |
| Southern Complex | | | | | |
| SYMBOLOPHORUS group | | | | | |
| *Bathylagus wesethi* | Bathylagidae | 5,593 | May–Sep (Jun) | T | MP (40–1,001 m) |
| *Cyclothone* spp. | Gonostomatidae | 5,869 | Aug–Oct (Aug) | WWC | MP |
| *Lampanyctus ritteri* | Myctophidae | 4,707 | Jan–Jul (May) | S-T to T | MP (MEP) |
| *Protomytophum crockeri* | Myctophidae | 8,048 | Dec–Apr (Mar) | T | MP (MEP) |
| *Symbolophorus californiensis* | Myctophidae | 3,219 | Apr–Jun (May) | T | MP (MEP) |
| *Trachurus symmetricus* | Carangidae | 5,612 | Mar–Jun (Jun) | T | EP (to 183 m) |

Table 1. Continued

| Recurrent group | Family | Occurrence | Peak abundance | Distribution | Adult habitat |
|---|---|---|---|---|---|
| TRIPHOTURUS group | | | | | |
| *Lampanyctus* spp. | Myctophidae | 5,481 | Feb–Aug (Apr) | S-T to Tr | MP to BP |
| *Triphoturus mexicanus* | Myctophidae | 11,968 | Jul–Sep (Aug) | SbT | MP (MEP) |
| CERATOSCOPELUS group | | | | | |
| *Ceratoscopelus townsendi* | Myctophidae | 3,058 | Jun–Sep (Aug) | WWC | MP (MEP) |
| *Diogenichthys atlanticus* | Myctophidae | 2,706 | Apr–May (Apr) | WWC | MP (MEP) |
| VINCIGUERRIA group | | | | | |
| *Diogenichthys laternatus* | Myctophidae | 5,043 | NT (Aug) | ETP | MP (MEP) |
| *Gonichthys tenuiculus* | Myctophidae | 1,234 | Feb–Mar (Feb) | ETP | MP (MEP) |
| *Hygophum atratum* | Myctophidae | 1,309 | NT (Nov) | ETP | MP (MEP) |
| *Vinciguerria lucetia* | Phosichthyidae | 10,510 | Jul–Oct (Aug) | ETP | MP (MEP) |
| Southern Coastal Complex | | | | | |
| SYNODUS group | | | | | |
| *Etrumeus teres* | Clupeidae | 502 | Aug–Oct (Aug) | SbT to Tr | EP |
| *Ophidion scrippsae* | Ophidiidae | 502 | Aug–Oct (Sep) | SbT to Tr | D (3–70 m) |
| *Prionotus* spp. | Triglidae | 363 | Aug–Oct (Sep) | SbT to Tr | D (15–110 m) |
| *Symphurus* spp. | Cynoglossidae | 1,038 | Aug–Oct (Aug) | SbT to Tr | D (1–201 m) |
| *Synodus* spp. | Synodontidae | 1,008 | Aug–Oct (Sep) | SbT to Tr | D (to 50 m) |

and range. During the 34-year period represented by the CalCOFI time series, the extensive population of *S. sagax* north of Point Conception nearly disappeared and the remainder was centered off coastal Baja California and in the Gulf of California (Ahlstrom, 1966; Smith and Moser, 1988). PARALICHTHYS is linked to CITHARICHTHYS through a significant affinity index between Sciaenidae and *E. mordax*. *P. californicus* inhabits shelf waters from central California to southern Baja California and spawns year-round with late winter and late summer peaks (Moser and Watson, 1990). Two species, *Genyonemus lineatus* and *Seriphus politus*, comprise most of the sciaenid larvae in CalCOFI samples (original data). They are nearshore species, ranging principally from central California to central Baja California and spawn at opposite times of the year with a winter peak for the former and a summer peak for the latter (Watson, 1982; Walker et al., 1987). As a composite, spawning range and seasonality for the two sciaenid species is similar to that of *P. californicus*.

SOUTHERN COMPLEX. The largest group of the Southern Complex, SYMBOLOPHORUS, consists of five mesopelagic taxa (*Symbolophorus californiensis, Lampanyctus ritteri, Protomyctophum crockeri, Bathylagus wesethi,* and *Cyclothone* spp.) and an epipelagic species, *Trachurus symmetricus* (Fig. 4, Table 1). Three mesopelagic taxa were associates of the group: *Melamphaes* spp. (linked with all group members except *L. ritteri*) and two taxa linked to *Cyclothone* spp., *Stomias atriventer* and the family Myctophidae (Fig. 4, Appendix). "Myctophidae" represents all myctophid larvae not identified to species because of their poor condition or small size. SYMBOLOPHORUS can be considered the core group of the California Current. *Bathylagus wesethi* is indigenous to the California Current. *Symbolophorus californiensis, P. crockeri, L. ritteri,* and *T. symmetricus* inhabit the California Current and range westward in the north Pacific transitional zone (Ahlstrom, 1969, 1972b; Moser and Ahlstrom, 1970; Wisner, 1976; Brodeur, 1988; Willis et al., 1988). *Symbolophorus californiensis* and *P. crockeri* reported from the western Pacific may be discontinuous with eastern Pacific populations (Willis et al., 1988). *Cyclothone* is primarily an equatorial-subtropical genus represented by at least seven species in the CalCOFI survey area, two of which (*C. signata* and *C. acclinidens*) are abundant in the California Current (Mukacheva, 1964). These two species constitute the bulk of the larvae taken in CalCOFI tows (original data). Abundance of larvae is highest in the spring or summer for members and associates of SYMBOLOPHORUS (Table 1). The Northern and Southern Complexes are linked only by the significant affinity index between *P. crockeri* (SYMBOLOPHORUS) and *S. leucopsarus* (LEUROGLOSSUS).

SYMBOLOPHORUS is connected directly and indirectly to the three other groups in the Southern Complex: TRIPHOTRUS, CERATOSCOPELUS, and VINCIGUERRIA (Fig. 4, Table 1). Both TRIPHOTURUS taxa (*Triphoturus mexicanus* and *Lampanyctus* spp.) have significant affinities with *Cyclothone* spp., *B. wesethi,* and *P. crockeri* of SYMBOLOPHORUS; *T. mexicanus* also has a significant link to *T. symmetricus* in the latter group. *T. mexicanus* is a subtropical species with greatest abundance in the southern extent of the California Current (Wisner, 1976). It spawns year-round with a peak in spring-summer (Ahlstrom, 1972b). *Lampanyctus* spp. includes larvae of more than a dozen species in the CalCOFI survey area that were not identified to species and also includes small (<5 mm) larvae of *L. ritteri.*

CERATOSCOPELUS is formed by two warm-water cosmopolites, *Diogenichthys atlanticus* and *Ceratoscopelus townsendi.* Both have significant affinities with *Cyclothone* spp. and *B. wesethi* of SYMBOLOPHORUS and *D. atlanticus* also has significant links to *P. crockeri* and *S. californiensis.* CERATOSCOPELUS is also connected to the TRIPHOTURUS group through a *C. townsendi-T. mex-*

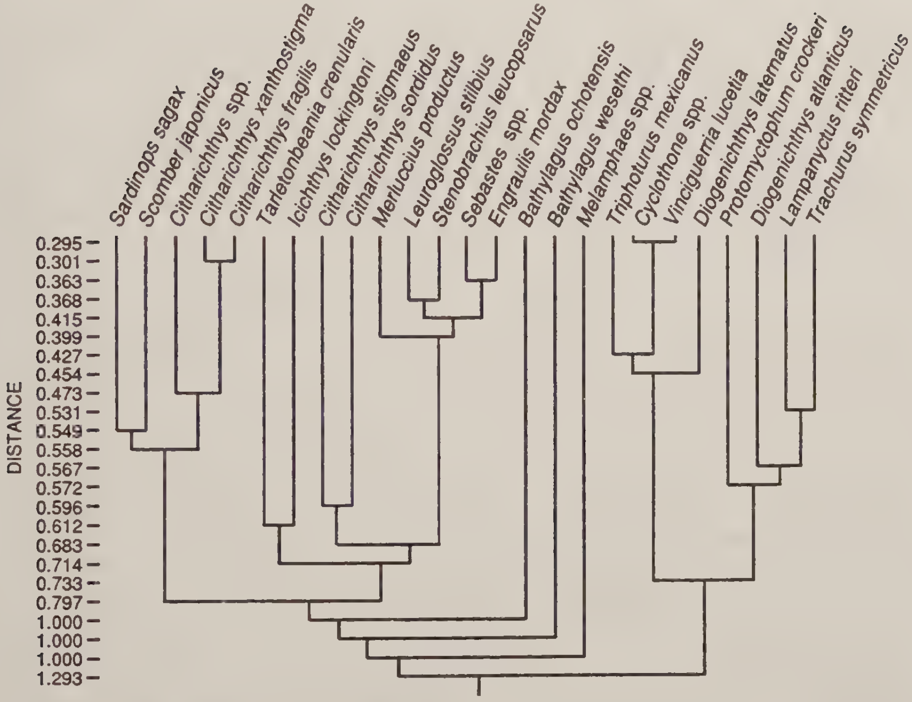

Figure 5. Cluster diagram showing results of an analysis of linear correlation of log-transformed abundances of the 25 most abundant larval fish taxa in the consistently sampled CalCOFI area during 1951 to 1984. Distances are expressed as 1 minus the correlation coefficient.

*icanus* linkage. Two other warm water cosmopolite myctophid species, *Lampadena urophaos* and *Notoscopelus resplendens,* are associates of CERATOSCOPELUS, through significant linkages with *C. townsendi* (Fig. 4, Table 1, Appendix).

VINCIGUERRIA consists of four eastern tropical Pacific (ETP) mesopelagic species: *Vinciguerria lucetia, Diogenichthys laternatus, Gonichthys tenuiculus,* and *Hygophum atratum.* The mesopelagic predator *Stomias atriventer* and Myctophidae are associates through links with *V. lucetia. Vinciguerria lucetia* and *D. laternatus* have significant affinities with both members of TRIPHOTURUS. VINCIGUERRIA is linked to SYMBOLOPHORUS through *V. lucetia-B. wesethi, V. lucetia-Cyclothone* spp., *V. lucetia-P. crockeri,* and *D. laternatus-Cyclothone* spp. and to CERATOSCOPELUS through *V. lucetia-C. townsendi* (Fig. 4, Table 1, Appendix).

SOUTHERN SHELF COMPLEX. This consists of the five-member recurrent group SYNODUS and three associate taxa (Fig. 4, Table 1). SYNODUS is composed of the epipelagic species, *Etrumeus teres,* and four demersal taxa (*Synodus* spp., *Prionotus* spp., *Symphurus* spp., and *Ophidion scrippsae*). Two percoid families, Carangidae and Serranidae, and the order Ophidiiformes (taxa other than *O. scrippsae* and *Chilara tayori*) are associates of the group. All had significantly affinity indices with *Prionotus* spp.; Ophidiiformes also was linked with *Synodus* spp. and Serranidae was linked with *Symphurus* spp. The member and associate taxa have broad tropical-subtropical distributions. Coincident samples of the group occurred only on the broad continental shelf region of central Baja California (Moser et al., 1987).

*Cluster Analysis.*—Cluster analysis produced two large groups, one composed of eight predominantly offshore taxa and the other composed of 14 taxa primarily with inshore distributions (Fig. 5). Three taxa (*Bathylagus ochotensis, B. wesethi,* and *Melamphaes* spp.) were uncorrelated.

The inshore grouping has two major subgroups: 1) a group of five taxa with distributions of larvae associated with the extensive shelf regions of southern California and Baja California, and 2) a group of nine taxa with more northerly distributions in coastal waters or seaward to the core of the California Current. In the shelf subgroup, *Sardinops sagax* and *Scomber japonicus* (the SARDINOPS group) are separated from a cluster of three paralichthyid taxa (*Citharichthys* spp., *C. fragilis,* and *C. xanthostigma*). The latter two species are the second most highly correlated pair in the entire dendrogram. The nine-taxon subgroup contains two species pairs and a highly correlated grouping of five taxa. One species pair is formed by *T. crenularis* and *I. lockingtoni* (the TARLETONBEANIA group), and the other consists of two sanddab species, *C. sordidus* and *C. stigmaeus,* with primarily cold water affinities. The five-species cluster is essentially the LEUROGLOSSUS recurrent group with *E. mordax* replacing *B. ochotensis.*

The offshore grouping consists of two four-member subgroups composed of taxa from the TRIPHOTURUS, VINCIGUERRIA, and SYMBOLOPHORUS recurrent groups of the Southern Complex. The first subgroup contains the pair, *Cyclothone* spp. and *V. lucetia,* the most highly correlated pair of taxa in the analysis. Although the taxa in this cluster represent three different recurrent groups (*T. mexicanus,* TRIPHOTURUS; *Cyclothone* spp., SYMBOLOPHORUS; *V. lucetia* and *D. laternatus,* VINCIGUERRIA), all taxon pairs in the cluster had significant affinity indices in the recurrent group analysis and all species have tropical or equatorial distributions. The other subgroup is composed of three taxa from SYMBOLOPHORUS (*P. crockeri, L. ritteri, T. symmetricus*) and one from the CERATOSCOPELUS group (*D. atlanticus*). The first three are primarily California Current species and *D. atlanticus* is a warm water cosmopolite that extends eastward into the California Current in the central region of the CalCOFI survey. Interestingly, *D. atlanticus* had a significant affinity index with *P. crockeri* in the recurrent group analysis but not with *L. ritteri* or *T. symmetricus.* In the cluster analysis *D. atlanticus* was more closely correlated with the latter two species.

*Principal Component Analysis.*—The first and second principal components explained 36% of the variation in the data (20.7 and 15.5%, respectively). The analysis revealed four distinct groups and several subgroups that identify north-south (ordinate) and inshore-offshore (abscissa) components as important variables (Fig. 6). Taxa comprising the Northern Complex of the recurrent group analysis have positive values on the ordinate while Southern Complex taxa have negative values. The upper right quadrant contains coastal demersal and pelagic taxa. All five of the sanddab taxa included in the analysis lie within that quadrant. *Citharichthys* spp. and the *C. fragilis-C. xanthostigma* pair lie to the extreme right, consonant with distributions concentrated over southern shelf areas. The more northern and offshore distributions of the other sanddab pair, *C. sordidus-C. stigmaeus,* are reflected in the plot. The *S. sagax-S. japonicus* pair lies in a similar position. A more northerly distribution is indicated for *E. mordax.*

The upper left quadrant contains the subarctic-transitional taxa that constitute LEUROGLOSSUS, the large recurrent group of the Northern Complex, and its closely connected species-pair group, TARLETONBEANIA. In the former, the two demersal taxa (*Sebastes* spp. and *M. productus*) have the lowest offshore position and *B. ochotensis* has the highest. *Stenobrachius leucopsarus* and *L.*

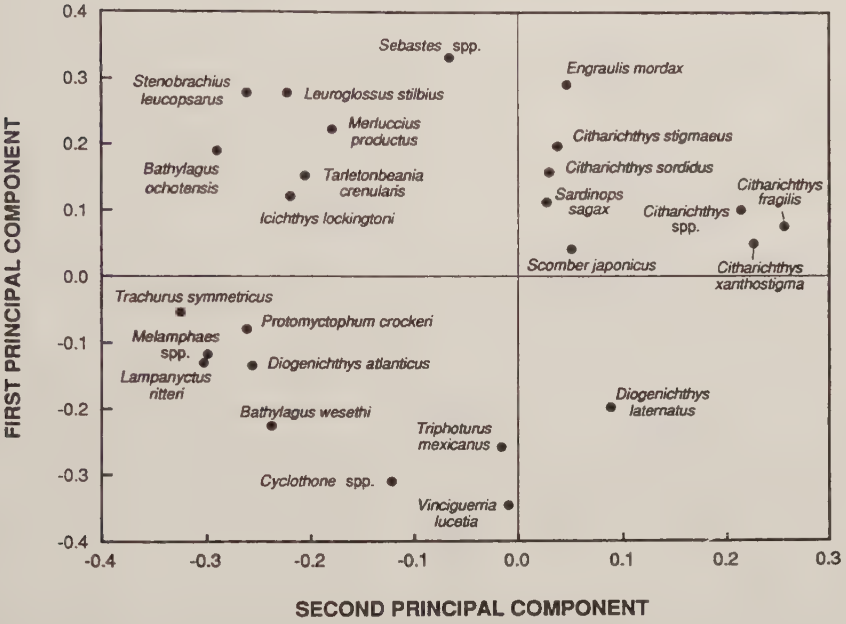

Figure 6. Plot of first and second principal component coefficients from an analysis of the 25 most abundant larval fish taxa in the consistently sampled CalCOFI area during 1954 to 1960.

*stilbius,* closely paired in recurrent group and cluster analyses, have an intermediate northerly location in the quadrant. *Tarletonbeania crenularis* and *I. lockingtoni* (TARETONBEANIA), have a more southerly position in the quadrant.

The lower left quadrant contains members of the four Southern Complex recurrent groups. A grouping of six taxa with offshore and relatively more northerly positions includes *T. symmetricus, P. crockeri, L. ritteri,* and *B. wesethi* of SYMBOLOPHORUS with the group associate *Melamphaes* spp. Also included in the grouping is *D. atlanticus* of the CERATOSCOPELUS group. The remaining taxa in the quadrant, *T. mexicanus, Cyclothone* spp., and *V. lucetia,* have more southerly positions and, with *D. laternatus* (the only taxon in the lower right quadrant), constitute a grouping that was also distinct in the cluster analysis.

## FRONTS 85 Cruise

*Horizontal Distribution.*—Bongo Net Samples. A total of 1,376 fish larvae representing 41 taxa was taken in 42 bongo-net tows on the south-north transect (Table 2). Taxa of the Northern Complex occurred infrequently and in low mean abundance. No LEUROGLOSSUS group member occurred in samples south of Station 5 and most were taken north of Station 6, the midpoint of the transect (Table 2). *Merluccius productus* was absent from the samples, since it has a restricted winter-spring spawning season (Table 1). *Tarletonbeania crenularis* larvae (TARLETONBEANIA group) declined markedly in abundance from north to south and were absent south of Station 6 (Fig. 7A). This distribution is consonant with historical data, since the southern extent of *T. crenularis* larvae in the CalCOFI time series is just south of the FRONTS 85 transect (Fig. 7B). *Diaphus* spp., an affiliate of TARLETONBEANIA (Appendix), occurred on all

Table 2. Total occurrences and mean number (per 10 m² surface area, positive tows) of larval taxa in bongo tows at 9 stations on the south-north transect of the FRONTS 85 cruise

| Taxon | Total occurrences | Stations | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| *Trachurus symmetricus* | 36 | 9.3 | 37.6 | 11.7 | 19.0 | 18.0 | 23.8 | 4.9 | 8.0 | 16.3 |
| *Triphoturus mexicanus* | 34 | 21.0 | 79.9 | 12.0 | 15.1 | 5.2 | 6.2 | 21.9 | 38.0 | 6.9 |
| *Diaphus* spp. | 33 | 4.7 | 5.0 | 14.4 | 11.9 | 20.5 | 16.3 | 7.3 | 18.6 | 35.7 |
| *Symbolophorus californiensis* | 33 | 13.4 | 14.1 | 7.2 | 8.0 | 5.1 | 5.0 | 9.8 | 12.1 | 5.5 |
| *Lampanyctus* spp. | 30 | 9.5 | 12.9 | 16.6 | 11.4 | 10.3 | 10.9 | 7.2 | 10.3 | 17.1 |
| *Bathylagus wesethi* | 28 | 9.6 | 41.7 | 9.7 | 18.0 | 36.1 | 9.8 | 4.7 | 16.3 | 15.9 |
| *Cyclothone* spp. | 27 | 6.7 | 30.7 | 9.4 | 15.1 | 5.2 | 4.9 | — | 7.9 | 7.1 |
| *Protomyctophum crockeri* | 26 | 8.2 | 10.3 | 7.2 | 12.6 | 10.3 | 9.9 | 7.3 | 7.9 | 12.8 |
| *Ceratoscopelus townsendi* | 24 | 9.6 | 34.1 | 11.7 | 12.6 | 10.2 | 10.6 | 4.7 | 6.4 | 4.6 |
| *Vinciguerria lucetia* | 24 | 30.1 | 69.8 | 102.1 | 80.1 | — | 5.0 | 4.8 | 4.5 | — |
| *Tarletonbeania crenularis* | 18 | — | — | — | — | 5.1 | 6.1 | 7.2 | 7.2 | 9.6 |
| *Melamphaes* spp. | 18 | 5.1 | 4.7 | 4.9 | 7.4 | 5.1 | 7.4 | 9.8 | 6.6 | 4.8 |
| *Lampanyctus regalis* | 17 | 4.5 | 9.6 | — | — | 5.2 | 7.4 | 9.4 | 4.3 | 11.3 |
| *Lestidiops ringens* | 13 | 7.3 | 7.8 | 9.7 | 5.2 | — | 4.8 | 4.9 | 8.9 | — |
| *Microstoma microstoma* | 10 | 7.0 | — | 4.9 | — | — | 4.8 | — | 4.4 | 4.8 |
| *Oxyjulis californica* | 10 | — | — | — | — | — | 10.2 | 14.1 | — | 9.6 |
| *Stomias atriventer* | 9 | 4.8 | 5.4 | 4.7 | 4.9 | — | — | 4.7 | — | — |
| *Engraulis mordax* | 8 | — | — | — | — | — | — | — | — | 6.5 |
| *Chauliodus macouni* | 8 | 4.7 | 5.7 | — | 4.9 | — | 5.0 | — | 4.2 | 8.2 |
| *Diogenichthys atlanticus* | 7 | 6.1 | 11.5 | — | — | — | — | 4.9 | — | 10.2 |
| *Scomber japonicus* | 6 | — | — | — | — | — | 5.0 | 4.7 | 4.6 | 4.6 |
| *Argyropelecus* spp. | 5 | 4.7 | 8.9 | — | — | 5.2 | — | — | 4.2 | 9.8 |
| *Bathylagus ochotensis* | 4 | — | — | — | — | 5.1 | — | 9.8 | — | 5.0 |
| *Sebastes* spp. | 4 | — | — | — | 4.9 | — | 5.0 | — | — | 4.8 |
| *Danaphos oculatus* | 2 | — | — | — | — | — | 4.9 | — | 4.5 | — |
| *Idiacanthus antrostomus* | 2 | — | — | — | 5.1 | — | — | — | 4.4 | — |
| *Stenobrachius leucopsarus* | 2 | — | — | — | — | — | 5.0 | — | — | — |
| *Etrumeus acuminatus* | 1 | — | — | — | — | — | — | — | — | 4.7 |
| *Nansenia candida* | 1 | — | — | — | — | — | 5.3 | — | — | — |
| *Leuroglossus stilbius* | 1 | — | — | — | — | — | 5.3 | — | — | — |
| *Sternoptyx* spp. | 1 | — | — | 4.9 | — | — | — | — | — | — |

Table 2. Continued

| Taxon | Total occur-rences | Stations | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| Stomiiformes | 1 | 4.9 | — | — | — | — | — | — | — | — |
| *Bathophilus flemingi* | 1 | 4.9 | — | — | — | — | — | — | — | — |
| *Notolepis risso* | 1 | — | — | — | — | — | — | — | — | 4.2 |
| *Benthalbella dentata* | 1 | — | 4.9 | — | — | — | — | — | — | — |
| *Rosenblattichthys volucris* | 1 | — | 4.4 | — | — | — | — | — | — | — |
| *Scopelosaurus harryi* | 1 | — | — | — | — | — | 4.9 | — | — | — |
| *Loweina rara* | 1 | — | — | — | 5.2 | — | — | — | — | — |
| *Cololabis saira* | 1 | — | — | — | — | — | 5.3 | — | — | — |
| *Trachipterus* spp. | 1 | — | — | — | — | — | — | — | — | 4.5 |
| *Icichthys lockingtoni* | 1 | — | — | — | — | — | 4.9 | — | — | — |
| Total larvae | | 94.7 | 339.5 | 214.2 | 206.5 | 105.4 | 112.7 | 103.6 | 146.4 | 133.7 |

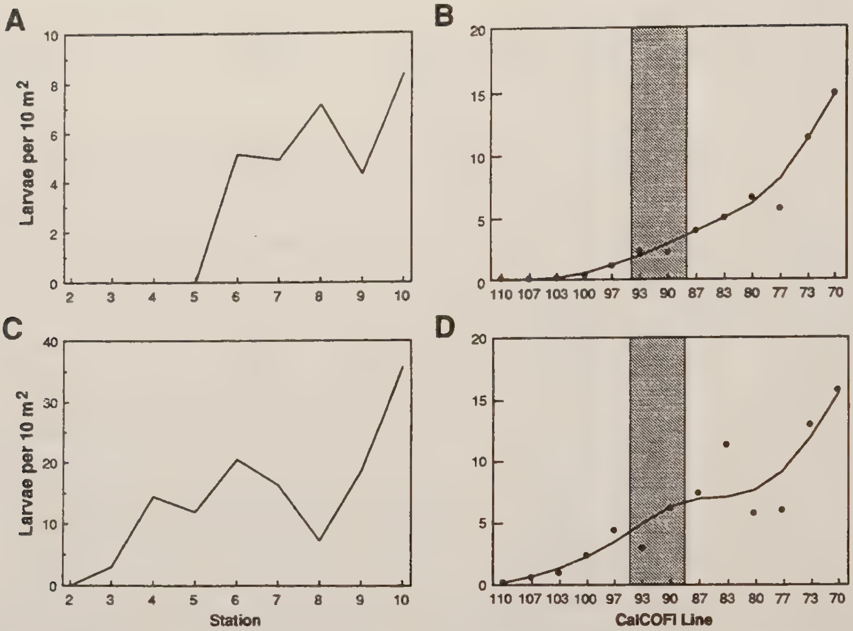

Figure 7. Change in mean abundance of two larval fish taxa representative of the Northern Complex from bongo-net tows at stations on the south-north FRONTS 85 transect (A, C) compared with long term latitudinal trends for the same taxa in 1,555 CalCOFI samples from that region (B, D). *Tarletonbeania crenularis* (A, B); *Diaphus* spp. (C, D). CalCOFI data points are arithmetic means of all stations in July and August between Stations 60 and 80 on 13 survey lines (Fig. 1). The line connects the results of a non-parametric smoother (Velleman, 1980). FRONTS 85 region is indicated by the shaded area on the CalCOFI graphs.

stations of the transect with a trend of decreasing abundance from north to south (Table 2, Fig. 7C.) In historical samples, *Diaphus* spp. larvae extend farther south than *T. crenularis* and long term mean abundance for *Diaphus* spp. in the FRONTS 85 sampling region is about twice that for *T. crenularis* (Fig. 7D). *Diaphus theta,* an abundant species of the subarctic-transitional north Pacific, was the principal, and perhaps only, species of the genus represented in the FRONTS 85 samples. Other taxa of the Northern Complex were too poorly represented to show any trend across the transect. *Scomber japonicus* (SARDINOPS group) had six occurrences, all in the northern half of the transect and *E. mordax* (CITHARICHTHYS group) had eight occurrences, all at the northernmost station (Table 2).

The bongo-net samples were dominated by larvae of the Southern Complex. Of the eight most frequently occurring taxa, five were SYMBOLOPHORUS group members (Table 2). Although most of the SYMBOLOPHORUS member taxa had their highest mean abundances at Station 3 in the southern half of the transect, only *B. wesethi* and *Cyclothone* spp. showed a clear trend of decreasing abundance from south to north (Table 2, Fig. 8). The historical data for *T. symmetricus* suggest a local peak in mean abundance in the FRONTS 85 region with a trend of increasing abundance to the north of the region (Fig. 8B). Historical data show that *B. wesethi* larvae decrease sharply in the FRONTS 85 region while *Cyclothone* abundance decreased abruptly south of the FRONTS 85 region (Fig. 8D, F).

*Vinciguerria lucetia* (VINCIGUERRIA group) had the greatest change in mean abundance of any species sampled, from 102 larvae per 10 m² at Station 4 to 0

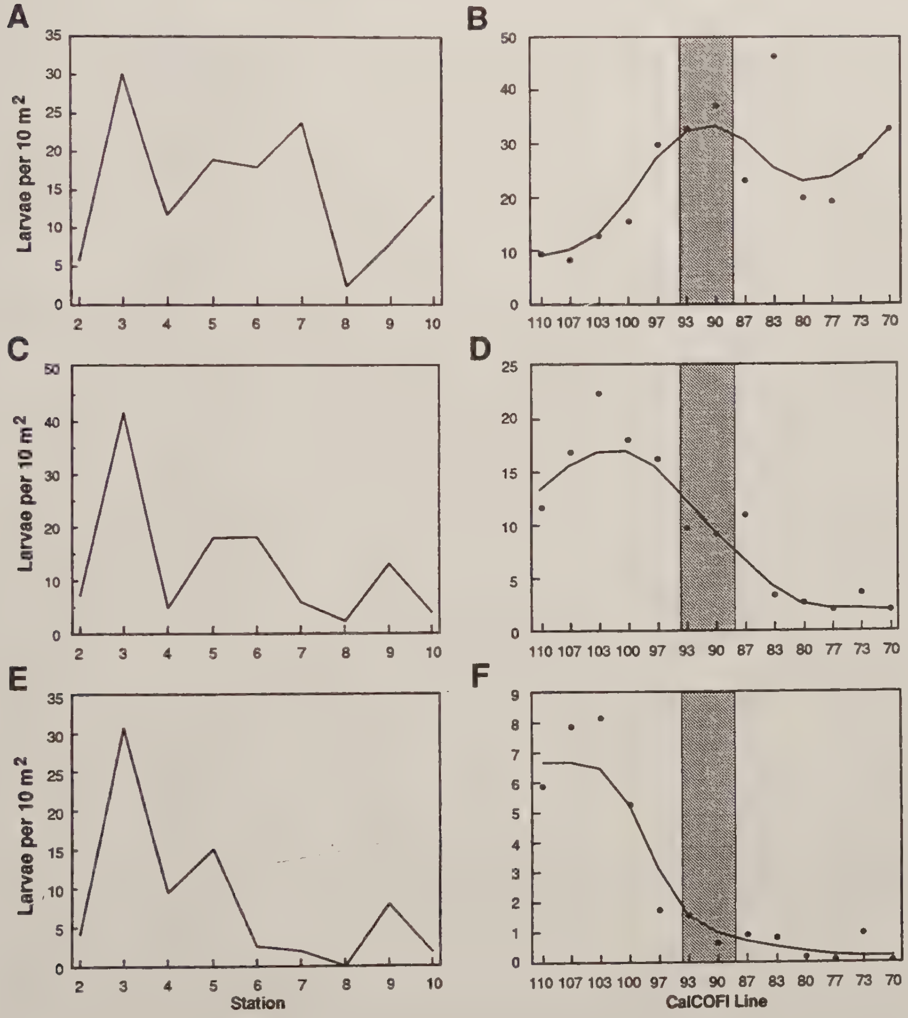

Figure 8. Change in mean abundance of three larval fish taxa representative of the Southern Complex from bongo-net tows at stations on the south-north FRONTS 85 transect (A, C, E) compared with long term latitudinal trends for the same taxa in 1,555 CalCOFI samples from that region (B, D, E). *Trachurus symmetricus* (A, B); *Bathylagus wesethi* (C, D); and *Cyclothone* spp. (E, F). Explanation as in Figure 7.

at mid-transect, and <5.0 per 10 m² at all other stations in the northern half of the transect (Table 2, Fig. 9A). Historical data show the FRONTS 85 region to be the northern terminus for larvae of this species (Fig. 9B). Similar but less dramatic trends were apparent for taxa in other Southern Complex groups. *Ceratoscopelus townsendi* (CERATOSCOPELUS) peaked at Station 3, declined sharply at Station 4, then continued its decline more gradually to the north (Table 2, Fig. 9C), while *T. mexicanus* (TRIPHOTURUS) showed a lesser peak at Station 9 in the northern part of the transect (Fig. 9E). Long term CalCOFI data for these species show an abrupt decline south of the FRONTS 85 region (Fig. 9D, F).

Measurements of environmental features along the transect reveal the frontal

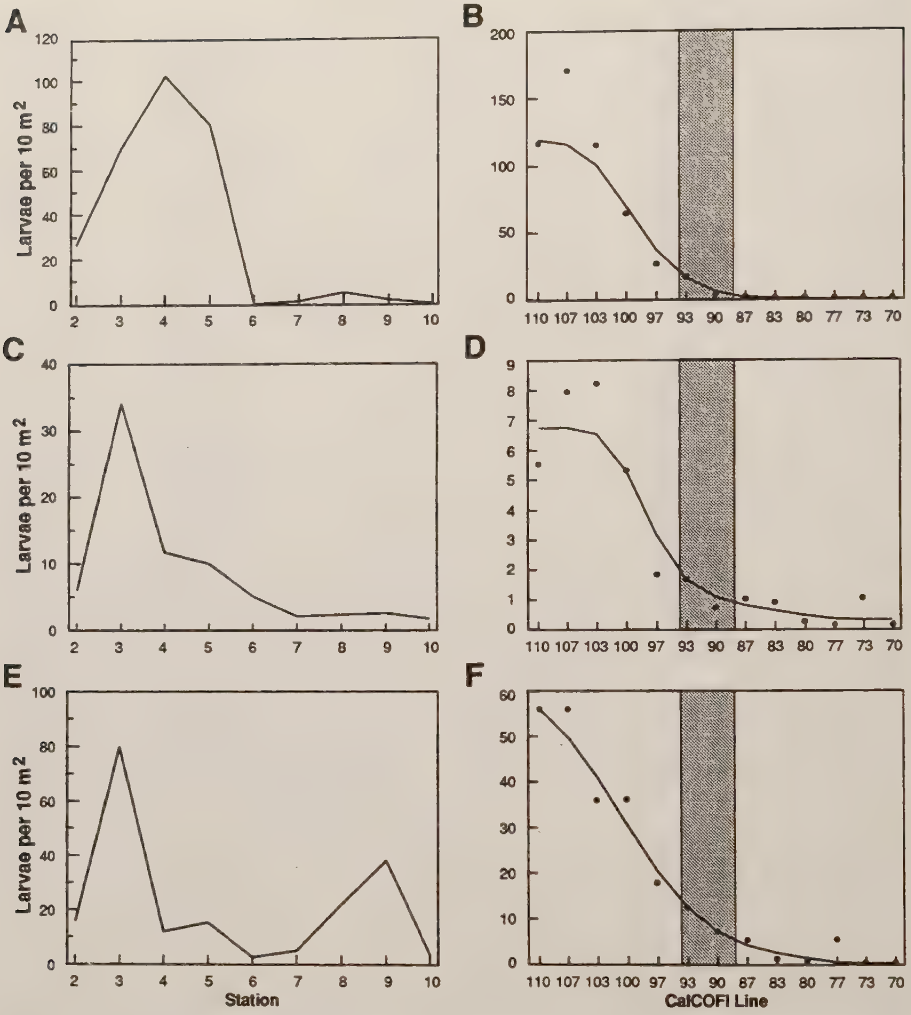

Figure 9. Change in mean abundance of three larval fish taxa representative of the Southern Complex from bongo-net tows at stations on the south-north FRONTS 85 transect (A, C, E) compared with long term latitudinal trends for the same taxa in 1,555 CalCOFI samples from that region (B, D, E). *Vinciguerria lucetia* (A, B); *Ceratoscopelus townsendi* (C, D); and *Triphoturus mexicanus* (E, F). Explanation as in Figure 7.

structure (Fig. 10). Sections of temperature, salinity, density, nitrate, oxygen saturation, and chlorophyll-*a* in the upper 250 m along the south-north transect show the shoaling of isopleths from south to north with rather sharp gradients at Stations 5 and 6 at the mid-transect. Niiler et al. (1989) and Haury et al. (1993) suggest that the tongue of low salinity water at 50–100 m in the southern half of the transect indicates subduction of northern water across the front (Fig. 10).

*Vertical Distribution.*—A total of 3,013 fish larvae representing 46 taxa was taken in 16 discrete depth strata on the 8 MOCNESS tows at both northern and southern

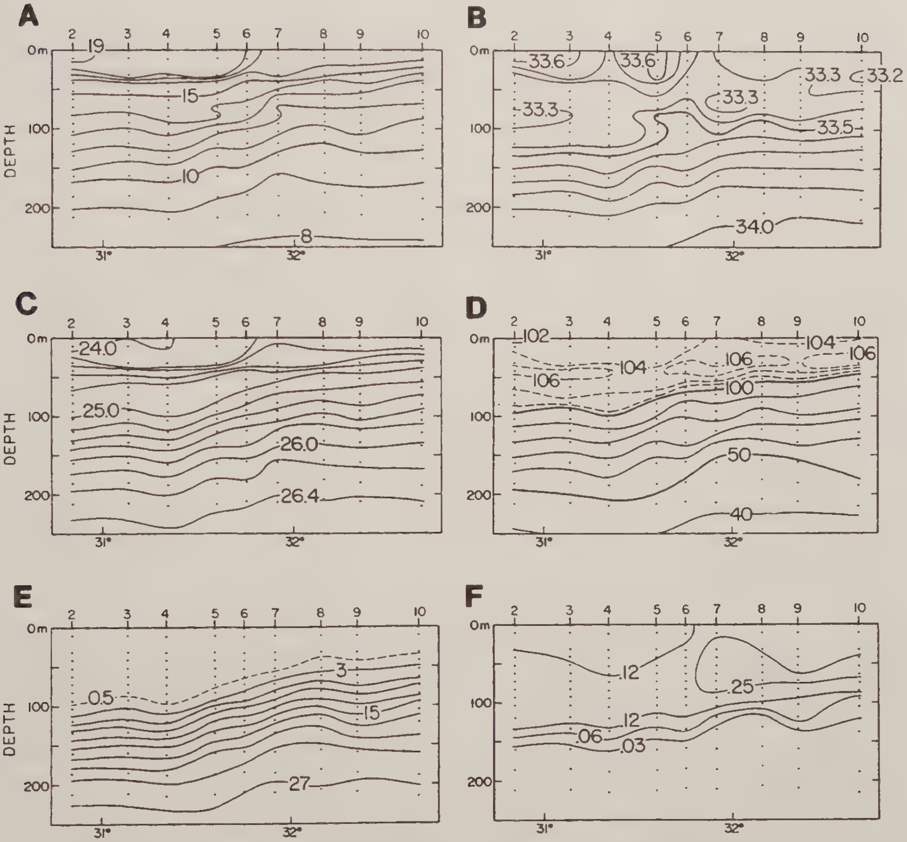

Figure 10. Sections to 250 m on the south-north transect of FRONTS 85 from Station 2 to Station 10: A, temperature (°C); B, salinity (‰); C, density ($kg \cdot m^{-3}$); D, oxygen concentration (% saturation); E, nitrate ($\mu m \cdot liter^{-1}$); F, chlorophyll-*a* ($mg \cdot m^{-3}$). Modified from Haury et al. (1986).

stations. Taxa of the Southern Complex accounted for 91% of the total occurrences at the southern station and for 42% at the northern station (Table 3). At the northern station, mean concentration of total larvae was highest at 25–75 m, whereas highest concentration was spread over a broader zone (25–100 m) at the southern station. Peak concentration at the northern station (25–50 m) was almost double that of the peak stratum (75–100 m) at the southern station, although mean abundance (number of larvae per 10 $m^2$ surface area) for all strata combined was only slightly higher in the north (Table 4).

Northern Complex. Taxa of the LEUROGLOSSUS recurrent group occurred only in samples from the northern station (Table 3, Fig. 11). All had low mean concentration, as would be expected of winter-spring spawners. They occurred moderately deep in the water column (*Sebastes* spp., 75–150 m; *S. leucopsarus,* 75–200 m; *L. stilbius,* 200–300 m; *B. ochotensis,* 75–400 m). The fifth member of the group, *M. productus* (not present in the samples), also deep living, occurs in or below the thermocline (Ahlstrom, 1959). *Tarletonbaenia crenularis* (TARLETONBEANIA) was relatively abundant at the northern station but absent from southern station samples; it occurred between 75 and 400 m, with peak concen-

Table 3. Total occurrences and mean number (per 1,000 m³, positive tows) of 46 larval fish taxa in MOCNESS tows at the north and south ends of the FRONTS 85 cruise transect

| Taxon | Total occurrences | South | | North | |
|---|---|---|---|---|---|
| | | Occurrences | Mean number | Occurrences | Mean number |
| *Lampanyctus* spp. | 36 | 20 | 7.7 | 16 | 41.0 |
| *Symbolophorus californiensis* | 32 | 22 | 10.7 | 10 | 14.2 |
| *Triphoturus mexicanus* | 29 | 23 | 54.1 | 6 | 32.7 |
| *Cyclothone* spp. | 25 | 24 | 18.0 | 1 | 7.7 |
| *Diaphus* spp. | 25 | 8 | 7.1 | 17 | 103.1 |
| *Bathylagus wesethi* | 24 | 19 | 27.3 | 5 | 22.0 |
| *Tarletonbeania crenularis* | 21 | — | — | 21 | 21.1 |
| *Trachurus symmetricus* | 21 | 11 | 37.7 | 10 | 50.2 |
| *Vinciguerria lucetia* | 20 | 20 | 62.1 | — | — |
| *Protomyctophum crockeri* | 19 | 6 | 6.7 | 13 | 13.7 |
| *Melamphaes* spp. | 18 | 9 | 7.7 | 9 | 8.4 |
| *Ceratoscopelus townsendi* | 17 | 17 | 20.6 | — | — |
| *Lampanyctus regalis* | 17 | 1 | 5.7 | 16 | 37.3 |
| *Microstoma microstoma* | 14 | 7 | 3.3 | 7 | 4.3 |
| *Lestidiops ringens* | 13 | 8 | 17.7 | 5 | 8.5 |
| *Argyropelecus* spp. | 11 | 1 | 1.1 | 10 | 3.4 |
| *Diogenichthys atlanticus* | 11 | 9 | 8.4 | 2 | 6.2 |
| *Chauliodus macouni* | 9 | 4 | 4.6 | 5 | 8.8 |
| *Oxyjulis californica* | 7 | — | — | 7 | 36.1 |
| *Sebastolobus altivelis* | 6 | — | — | 6 | 4.9 |
| *Danaphos oculatus* | 5 | 1 | 1.6 | 4 | 5.1 |
| *Stomias atriventer* | 5 | 5 | 6.0 | — | — |
| *Sebastes* spp. | 5 | — | — | 5 | 10.2 |
| *Scomber japonicus* | 5 | — | — | 5 | 10.7 |
| *Engraulis mordax* | 4 | 1 | 4.5 | 3 | 53.4 |
| *Bathylagus ochotensis* | 4 | — | — | 4 | 5.0 |
| *Leuroglossus stilbius* | 3 | — | — | 3 | 5.4 |
| *Sternoptyx* spp. | 3 | 2 | 5.0 | 1 | 1.7 |
| *Scopelosaurus harryi* | 3 | 2 | 4.2 | 1 | 9.0 |
| *Stenobrachius leucopsarus* | 3 | — | — | 3 | 6.7 |
| *Trachipterus* spp. | 3 | — | — | 3 | 7.0 |
| *Idiacanthus antrostomus* | 2 | 1 | 2.3 | 1 | 7.7 |
| *Scopelarchus* sp. | 2 | 2 | 5.5 | — | — |
| *Citharichthys stigmaeus* | 2 | — | — | 2 | 6.4 |
| *Nansenia candida* | 1 | — | — | 1 | 6.2 |
| *Tactostoma macropus* | 1 | 1 | 5.7 | — | — |
| Melanostomiidae | 1 | 1 | 7.1 | — | — |
| *Chilara taylori* | 1 | — | — | 1 | 18.0 |
| *Poromitra* spp. | 1 | — | — | 1 | 5.6 |
| *Scopelogadus bispinosus* | 1 | 1 | 7.7 | — | — |
| *Sebastolobus alascanus* | 1 | — | — | 1 | 2.7 |
| *Paralabrax* spp. | 1 | — | — | 1 | 7.1 |
| Chiasmodontidae | 1 | 1 | 6.4 | — | — |
| Gobiidae | 1 | — | — | 1 | 9.0 |
| *Tetragonurus cuvieri* | 1 | 1 | 11.8 | — | — |
| *Citharichthys sordidus* | 1 | — | — | 1 | 9.0 |

tration in strata between 75 and 150 m (Table 3, Fig. 12A). An affiliate, *Diaphus* spp., had a shallower distribution with the highest mean concentration (103 larvae per 1,000 m³) of any taxon in the MOCNESS samples (Fig. 12B, Table 3). *Scomber japonicus* (SARDINOPS) occurred in low abundance in the upper 100 m of the northern samples, with highest concentration at 25–50 m (Fig. 12C). *Engraulis mordax* (CITHARICHTHYS) occurred in one sample at the southern station and in three samples in the north, with a peak at 25–50 m (Fig. 12D).

Table 4. Mean volume ($m^3$) of water filtered and mean number (per 1,000 $m^3$) of total fish larvae in 16 strata sampled by 8 MOCNESS tows (4 north, 4 south) on the FRONTS 85 cruise. For the entire water column, total fish larvae divided by total water filtered is expressed as number per 1,000 $m^3$; total larvae per 10 $m^2$ of surface areas is in parentheses.

| | North | | South | |
|---|---|---|---|---|
| Depth (m) | Mean volume filtered | Mean total larvae | Mean volume filtered | Mean total larvae |
| 0–25 | 142 | 30.6 | 151 | 50.6 |
| 25–50 | 134 | 490.4 | 169 | 230.5 |
| 50–75 | 141 | 423.5 | 174 | 260.0 |
| 75–100 | 123 | 284.2 | 169 | 268.3 |
| 100–125 | 112 | 147.4 | 208 | 184.2 |
| 125–150 | 168 | 62.1 | 185 | 88.4 |
| 150–175 | 149 | 32.9 | 238 | 93.9 |
| 175–200 | 142 | 8.8 | 206 | 73.2 |
| 200–225 | 203 | 46.2 | 177 | 22.8 |
| 225–250 | 112 | 24.1 | 153 | 27.2 |
| 250–300 | 237 | 32.1 | 249 | 15.7 |
| 300–400 | 412 | 13.0 | 394 | 13.7 |
| 400–550 | 595 | 8.3 | 631 | 1.8 |
| 550–700 | 531 | 1.7 | 533 | 0.9 |
| 700–850 | 483 | 2.8 | 522 | 1.5 |
| 850–1,000 | 551 | 5.1 | 592 | 1.4 |
| 0–1,000 | | 50.2<br>(431) | | 51.2<br>(349) |

Southern Complex. All taxa of the SYMBOLOPHORUS recurrent group, except *L. ritteri,* were identified in samples from northern and southern localities and ranked among the 10 most frequently occurring taxa overall (Table 3). SYMBOLOPHORUS taxa had diverse vertical distribution patterns. Occurrences of *T. symmetricus* larvae were about equal at both localities and were restricted to the upper 100 m with a marked peak at 25–50 m, where mean concentration was twice as great in the north compared with the south (Fig. 13A). *Symbolophorus californiensis* had twice as many occurrences in the south as in the north and occupied a broad depth range (25–300 m) at both stations; however mean concentration was greater in deep strata at the southern station compared with the northern station (Fig. 13B). This shift in depth distribution at the two localities was even more apparent in *B. wesethi* (Fig. 13C). Occurrences of *B. wesethi* were four times greater in the south, where larvae ranged from 75 to 250 m depth with a concentration peak at 150–175 m. In the north they ranged from 50 to 125 m with a peak at 75–100 m. *Protomyctophum crockeri* larvae occurred twice as frequently in the north compared with the south and had a markedly deeper distribution than other SYMBOLOPHORUS group members (Table 3, Fig. 13D). In the north they ranged from 175 to 550 m with a peak at 200–225 m, while in the south they ranged from 225 to 550 m with a peak at 300–400 m. *Cyclothone* spp. was fourth in overall incidence with all but one occurrence at the southern site (Table 3). All larvae were taken in the upper 200 m with a distinct peak at 75–100 m (Fig. 14A).

Shoaling of vertical distributions at the northern station was also apparent for associates of SYMBOLOPHORUS. *Melamphaes* spp. occurred in low abundance with a peak at 75–100 m in the north and at 150–175 m in the south (Table 3, Fig. 14B). The paralepidid *Lestidiops ringens,* a SYMBOLOPHORUS affiliate (Appendix), had non-overlapping vertical ranges at the two sites with peak concentration at 50–75 m in the north and at 175–200 m in the south (Fig. 14C).

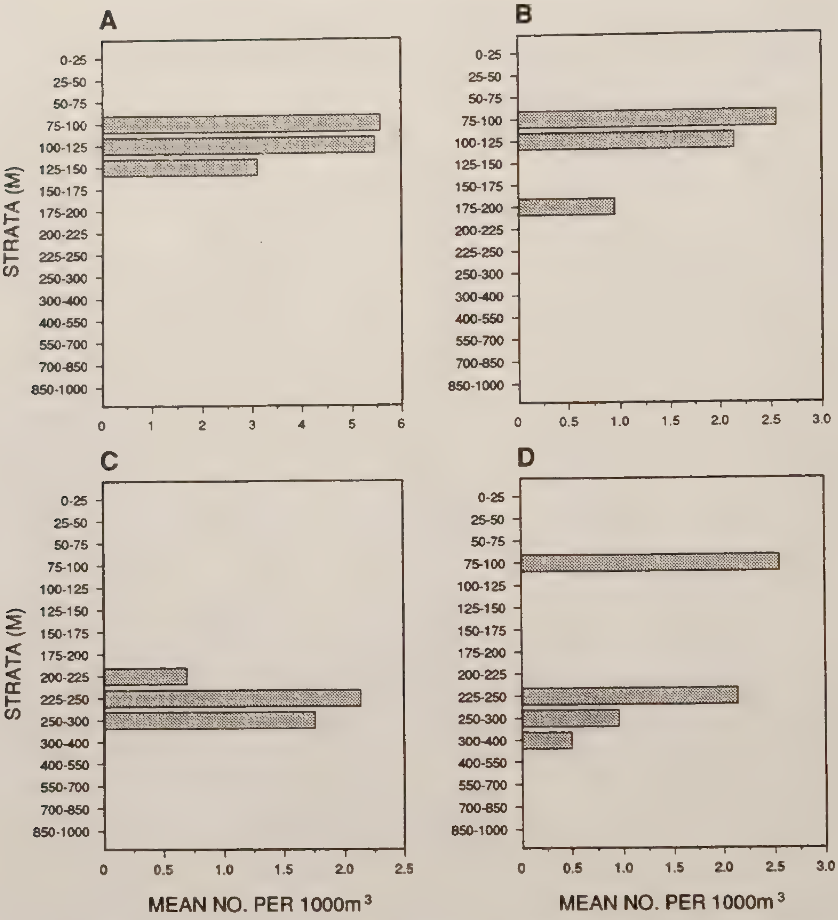

Figure 11. Depth distribution of larvae of four members of the Northern Complex recurrent group LEUROGLOSSUS from MOCNESS samples taken on northern end of the FRONTS 85 transect. A, *Sebastes* spp.; B, *Stenobrachius leucopsarus*; C, *Leuroglossus stilbius*; D, *Bathylagus ochotensis*.

Another affiliate, *Microstoma microstoma,* occurred deep in the water column at each site with concentration maxima at 200–225 m in north and at 300–400 m in the south (Fig. 14D).

*Vinciguerrua lucetia* (VINCIGUERRIA) occurred only at the southern locality and in high frequency and relative abundance (Table 3). Except for a few late stage specimens, the larvae were restricted to the upper 150 m with a sharp peak at 50–75 m (Fig. 15A). Other VINCIGUERRIA members (*D. laternatus, G. tenuiculus, H. atratum*) not present in FRONTS 85 samples are known to have comparatively deep distributions (Loeb and Nichols, 1984). *Stomias atriventer,* an associate of the group, occurred in 5 samples in the upper 200 m at the southern site (Table 3, Fig. 15B).

Both members of the CERATOSCOPELUS group were present in the MOCNESS samples. *Ceratoscopelus townsendi* occurred only at the southern station in the upper 175 m, with a peak at 25–50 m (Table 3, Fig. 15C). Captures of *D.*

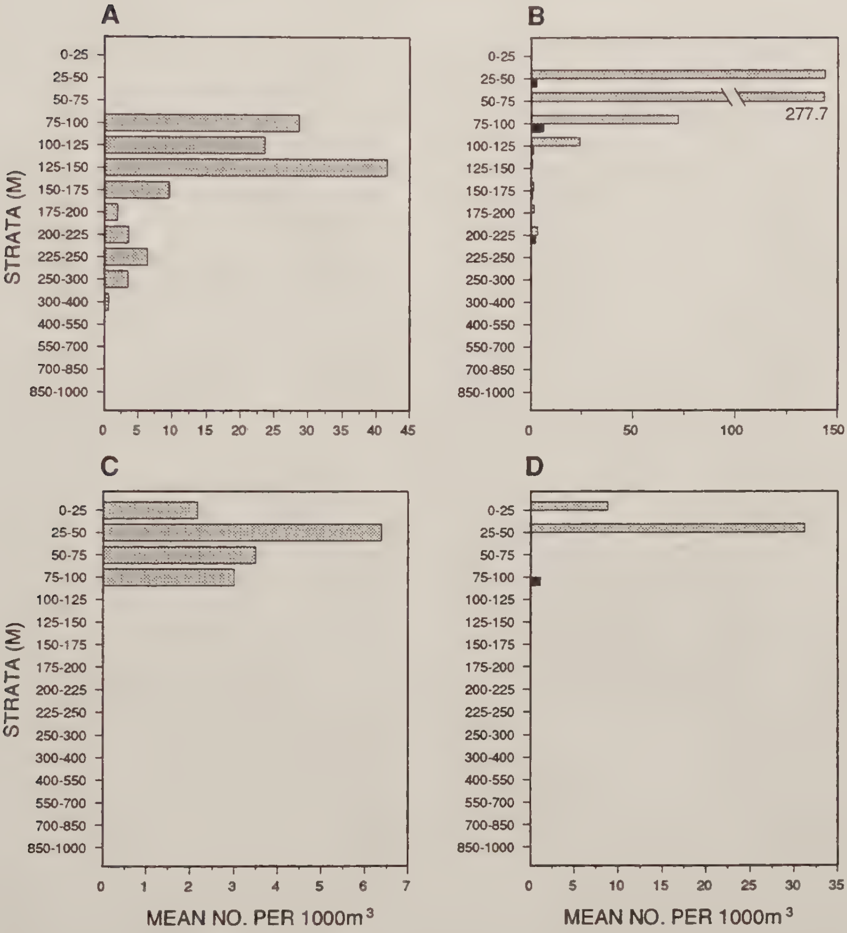

Figure 12. Depth distribution of larvae of four taxa of the Northern Complex from MOCNESS samples taken on FRONTS 85. A, *Tarletonbeania crenularis*; B, *Diaphus* spp.; C, *Scomber japonicus*; D, *Engraulis mordax*. Mean larval fish abundances versus depth are shown for tows at the northern end of the transect (light bars) and for the southern end (dark bars).

*atlanticus* were mostly at the southern station in a broader and deeper depth band (50 to 300 m) compared with *C. townsendi,* with no apparent peak (Fig. 15D).

At the southern station, *T. mexicanus* (TRIPHOTURUS) had a distribution similar to that of *V. lucetia* with a peak at 50–75 m. Incidence and abundance were markedly lower at the northern station and the distribution was shifted upward with a peak in the 25–50-m stratum (Fig. 16A). The other TRIPHOTURUS member, *Lampanyctus* spp., had the highest number of occurrences of any taxon in the MOCNESS samples (Table 2). Occurrence was slightly higher in the south; however, mean abundance was higher in the north. Larvae occurred over a broad depth range (25 to 300 m), with low concentrations in strata >125 m in the north and in all strata in the south (Fig. 16B).

Larvae of two mesopelagic predators, *Chauliodus macouni* and *Scopelosaurus harryi,* occurred at both north and south localities and had broad, disjointed

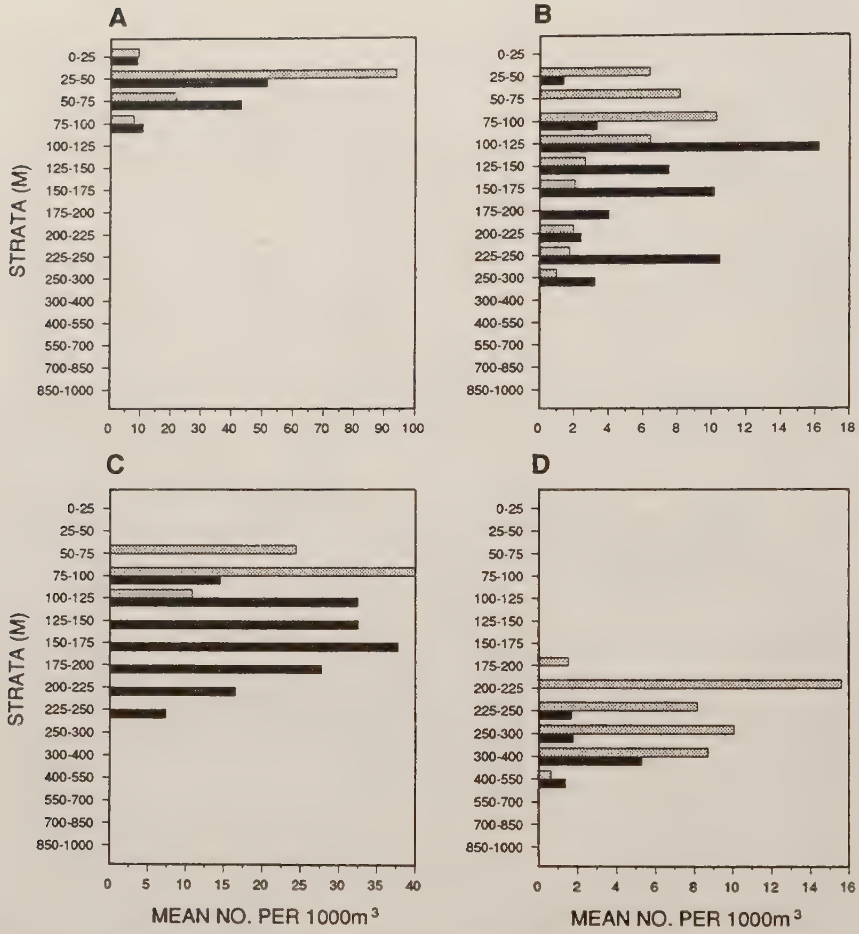

Figure 13. Depth distribution of larvae of four members of the Southern Complex recurrent group SYMBOLOPHORUS from MOCNESS samples taken on FRONTS 85. A, *Trachurus symmetricus*; B, *Symbolophorus californiensis*; C, *Bathylagus wesethi*; D, *Protomyctophum crockeri*. Symbols as in Figure 12.

vertical distributions (Fig. 16C, D). *Chauliodus macouni,* an affiliate of TARLETONBEANIA (Appendix), occurred in two widely separated groups of strata, with no captures in the 100 to 200 m range (Fig. 16D). *Scopelosaurus harryi,* a CERATOSCOPELUS affiliate (Appendix), occurred in only three samples but in widely separated strata at the north and south sites (Fig. 16D). Two sternoptychid taxa affiliated with SYMBOLOPHORUS, *Danaphos oculatus* and *Argyropelecus* spp., had the deepest distributions encountered in the MOCNESS samples. *D. oculatus* was distributed between 400 and 1,000 m with a peak at 400–550 m (Fig. 17A) and *Argyropelecus* spp. was found between 300 and 1,000 m with a peak at 850–1,000 m (Fig. 17B).

ENVIRONMENTAL OBSERVATIONS. Hydrographic conditions differed markedly at the two MOCNESS stations indicative of the separate water masses. Surface temperature was 16.2°C at Station 10 in the north and 19.0°C at Station 2 in the

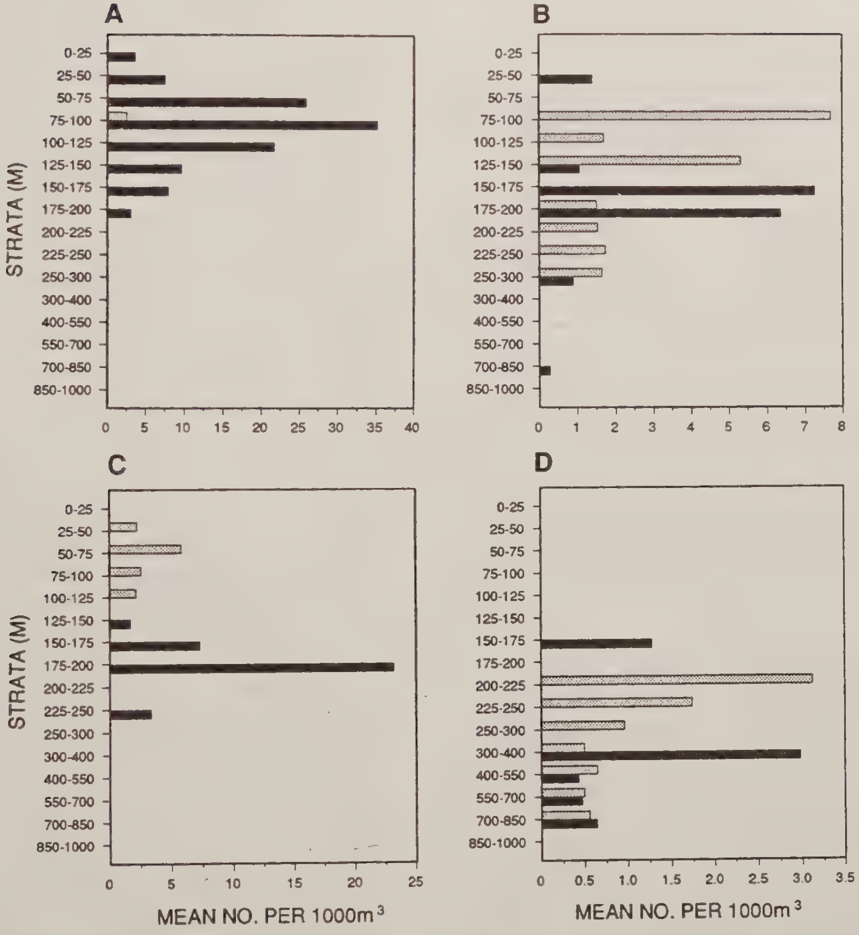

Figure 14. Depth distribution of larvae of group members (A), associates (B), and affiliates (C, D) of the Southern Complex recurrent group SYMBOLOPHORUS from MOCNESS samples taken on FRONTS 85. A, *Cyclothone* spp.; B, *Melamphaes* spp.; C, *Lestidiops ringens*; D, *Microstoma microstoma*. Symbols as in Figure 12.

south. A differential of 3–4°C was maintained down to circa 100 m (Fig. 18A). Surface salinity was 0.3‰ higher at the southern station, then became lower by circa 0.2‰ at the southern station between 60 and 200 m, possibly indicating subduction of water from the north (Fig. 18B). Dissolved oxygen was slightly higher at the surface in the north but below circa 50 m was consistently lower at the northern station (Fig. 18C). The temperature-salinity relationship indicates the colder less saline nature of the shallow water at the northern station compared with the southern station (Fig. 18D).

Nutrient and pigment concentrations differed markedly north (Station 10) and south (Station 2) of the front. Phosphate concentration was higher at comparable depths in the north, with the greatest difference in the upper 200 m (Fig. 19A). Similarly, nitrate concentrations were different at the two stations down to approximately 400 m (Fig. 19B). The chlorophyll maximum was at 50 m in the

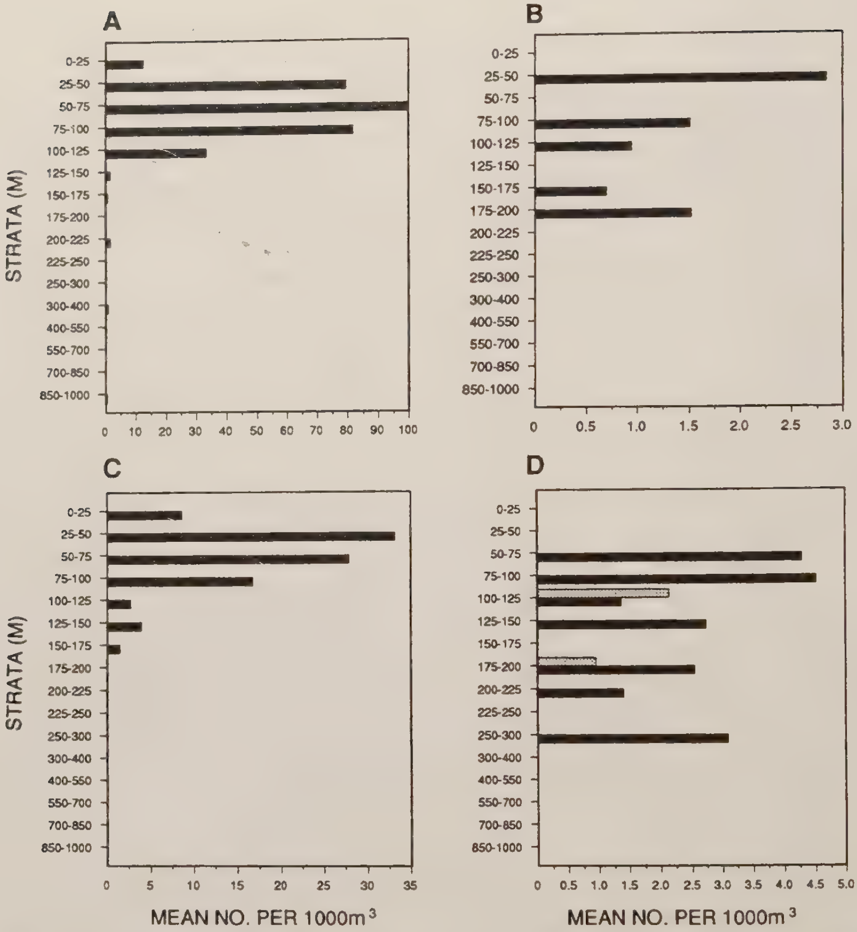

Figure 15. Depth distribution of larvae of a member (A) and an associate (B) of the Southern Complex recurrent group VINCIGUERRIA and two members of the Southern Complex recurrent group CERATOSCOPELUS (C, D) from MOCNESS samples taken on FRONTS 85. A, *Vinciguerria lucetia*; B, *Stomias atriventer*, C, *Ceratoscopelus townsendi*; D, *Diogenichthys atlanticus*. Symbols as in Figure 12.

north and at 100 m in the south (Fig. 19D). The depth curve for phaeophytin showed a similar contrast between the two stations (Fig. 19D). Primary production was circa 3.5 times greater in the north compared with the south, reaching a maximum uptake rate of almost 7 mg carbon$\cdot$m$^{-3}\cdot$half-day$^{-1}$ experiment at 25 m in the north (Fig. 20). Standing crop of macrozooplankton was higher throughout the water column in the north (Fig. 21). In the south, displacement volume varied between 100 and 200 cm$^3\cdot$1,000 m$^{-3}$ at strata from the surface to 250 m and was $<$100 cm$^3\cdot$1,000 m$^{-3}$ at deeper strata. In the north, displacement volume was 600 to 800 cm$^3\cdot$1,000 m$^{-3}$ in the upper 50 m, four to six times greater than at that depth range in the south. Light penetration differed greatly north and south of the front; the 1% level of surface light was 20 to 25 m deeper at the southern station, 85 to 86 m in the south vs. 61 to 65 m in the north (Fig. 22).

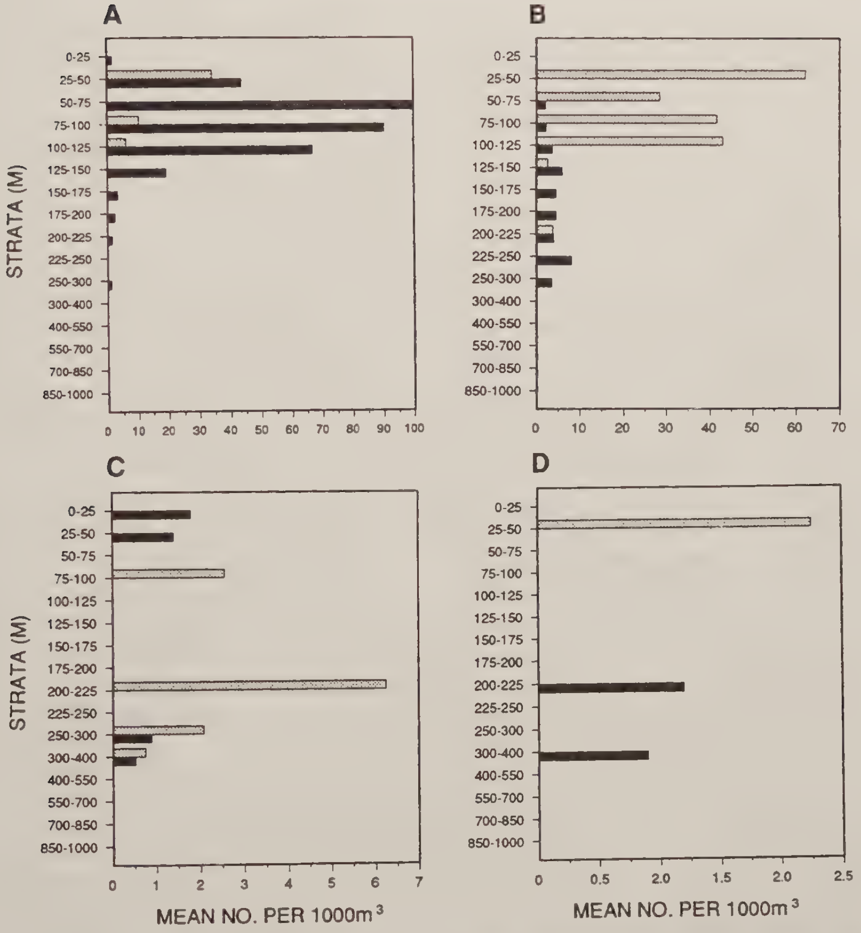

Figure 16. Depth distribution of larvae of two members of the Southern Complex recurrent group TRIPHOTURUS (A, B) and of two taxa of mesopelagic predators (C, D) from MOCNESS samples taken on FRONTS 85. A, *Triphoturus mexicanus*; B, *Lampanyctus* spp.; C, *Chauliodus macouni*; D, *Scopelosaurus harryi*. Symbols as in Figure 12.

The environmental changes experienced by taxa that occurred on both sides of the front are shown by larva-weighted mean values for depth and associated hydrographic and biological parameters (Table 5). The shallow living *T. symmetricus* and *T. mexicanus* changed the least, and generally, the difference between the two localities increased in deeper living taxa. Larva-weighted mean temperature decreased substantially in *T. symmetricus* and *T. mexicanus* in the north while, in most other taxa, it increased at the northern station because they occurred at shallower depths north of the front. Larva-weighted density values increased in *T. symmetricus* and *T. mexicanus* at the northern station while they decreased from south to north in the deeper living taxa because of the shoaling of their distributions. Larva-weighted salinity was slightly lower in the north for most species. In *T. symmetricus* and *T. mexicanus* this is due to the lower salinities in the upper 75 m at the northern station. The deeper living taxa experienced lower

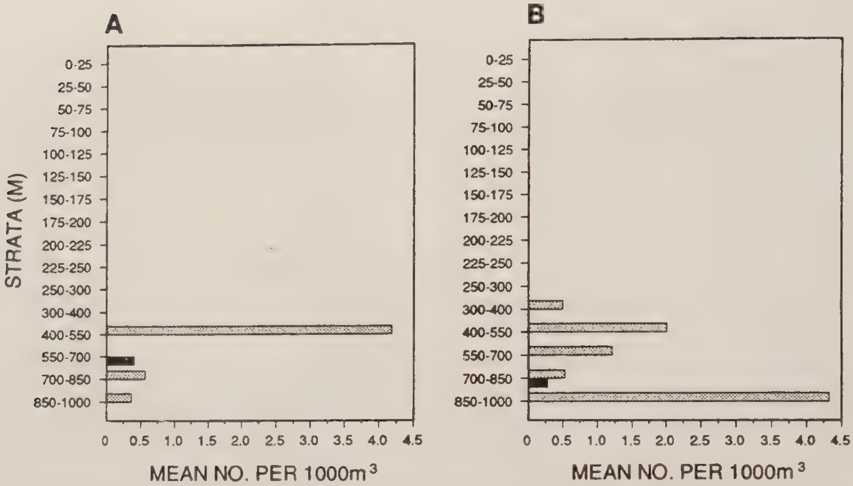

Figure 17. Depth distribution of larvae of two sternoptychid taxa from MOCNESS samples taken on FRONTS 85. A, *Danaphos oculatus*; B, *Argyropelecus* spp. Symbols as in Figure 12.

salinities at their shallower habitat in the north (Table 5, Fig. 18B). In *T. symmetricus,* the slight increase in the larva-weighted mean for dissolved oxygen at the northern station was related to higher levels in surface waters there (Fig. 18C). Higher values for the other taxa at the northern station resulted from the change in oxygen concentration with depth (Fig. 18C) and shoaling of their distributions north of the front (Table 5).

Larva-weighted mean chlorophyll-*a* concentrations were higher north of the front for all taxa, despite the highly disparate chlorophyll-*a* profiles at the two sites (Table 5, Fig. 19C). The shift was smallest for *T. mexicanus* whose mean depth distributions were near the chlorophyll maxima at each site. *Lestidiops ringens* experienced a 1,900% increase from south to north, since its mean depth was well below the euphotic zone south of the front but near the chlorophyll-*a* maximum at the northern site (Table 5, Fig. 19C). Likewise, larva-weighted zooplankton displacement volumes were markedly higher north of the front for all taxa, with increases ranging from 114% in *Microstoma microstoma,* the deepest living taxon, to 400% in the shallow living *T. symmetricus. Lestidiops ringens* had the largest shift (427%) because of its extreme change in vertical distribution (Table 5, Fig. 21).

## Discussion and Conclusions

Recurrent group analysis of the entire CalCOFI time series identified an assemblage of larval fish groups whose composition and structure were generally consistent with those derived from portions of the time series and with groupings based on principal component and cluster analyses of abundance data. These groups reflect the major water masses and boundary regions present in the California Current region.

The California Current, generated from the West Wind Drift off Washington and Oregon, carries subarctic-transitional water southward. Larval fish assemblages off Washington and Oregon are dominated by the myctophids *S. leucopsarus, T. crenularis,* and *D. theta,* the bathylagid *B. ochotensis,* and the scorpaenid

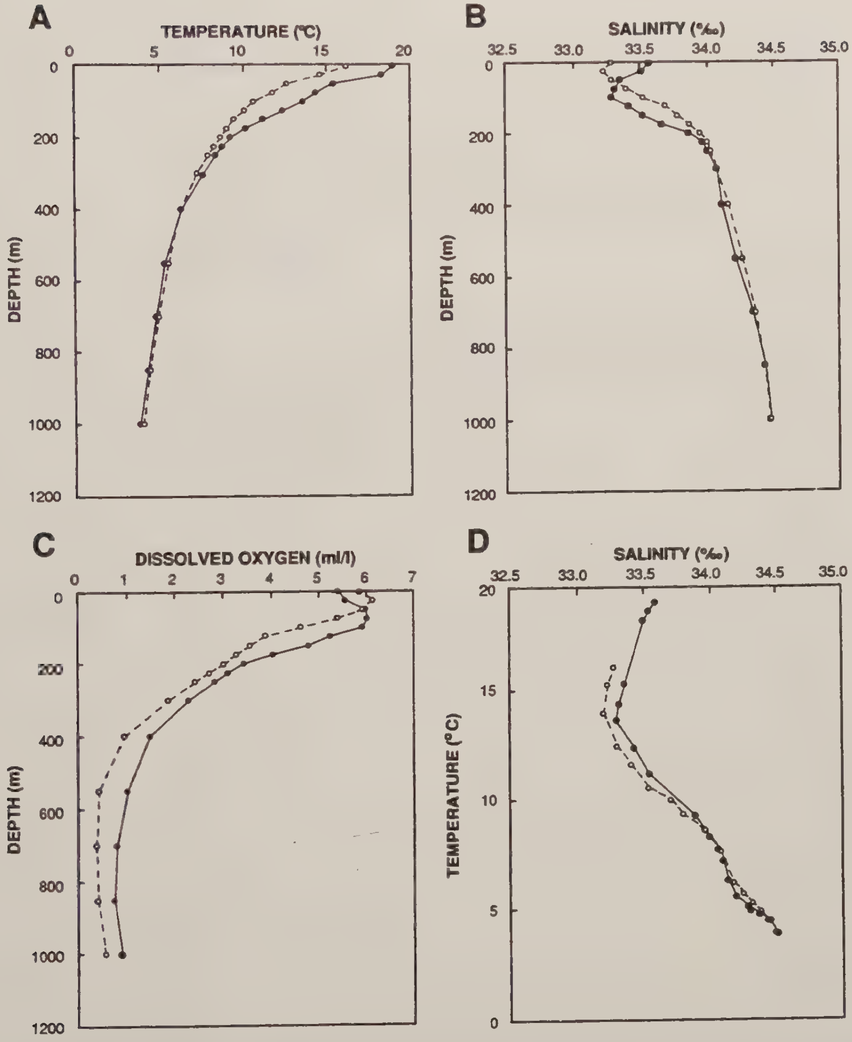

Figure 18. Temperature (A), salinity (B), and dissolved oxygen (C) depth profiles and T-S diagrams (D) for Station 2, Cast 8 at the southern end of the FRONTS 85 transect (closed circles) and for Station 10, Cast 1 at the northern end (open circles). Data from Haury et al. (1986).

genus *Sebastes* (Doyle et al., this volume). These taxa are prominent members of the Northern Complex of recurrent larval fish groups in the CalCOFI survey area; *S. leucopsarus, B. ochotensis,* and *Sebastes,* with *M. productus* and another bathylagid (*L. stilbius*), form LEUROGLOSSUS, the major recurrent group of the Northern Complex.

South of Point Conception, the California Current bends shoreward; part of the flow heads north to form the Southern California Eddy and part continues south along Baja California. Off northern Baja California, central and ETP water impinge on the California Current from the west and south, respectively. Mesopelagic taxa dominate the larval fish assemblages of these water masses (Loeb,

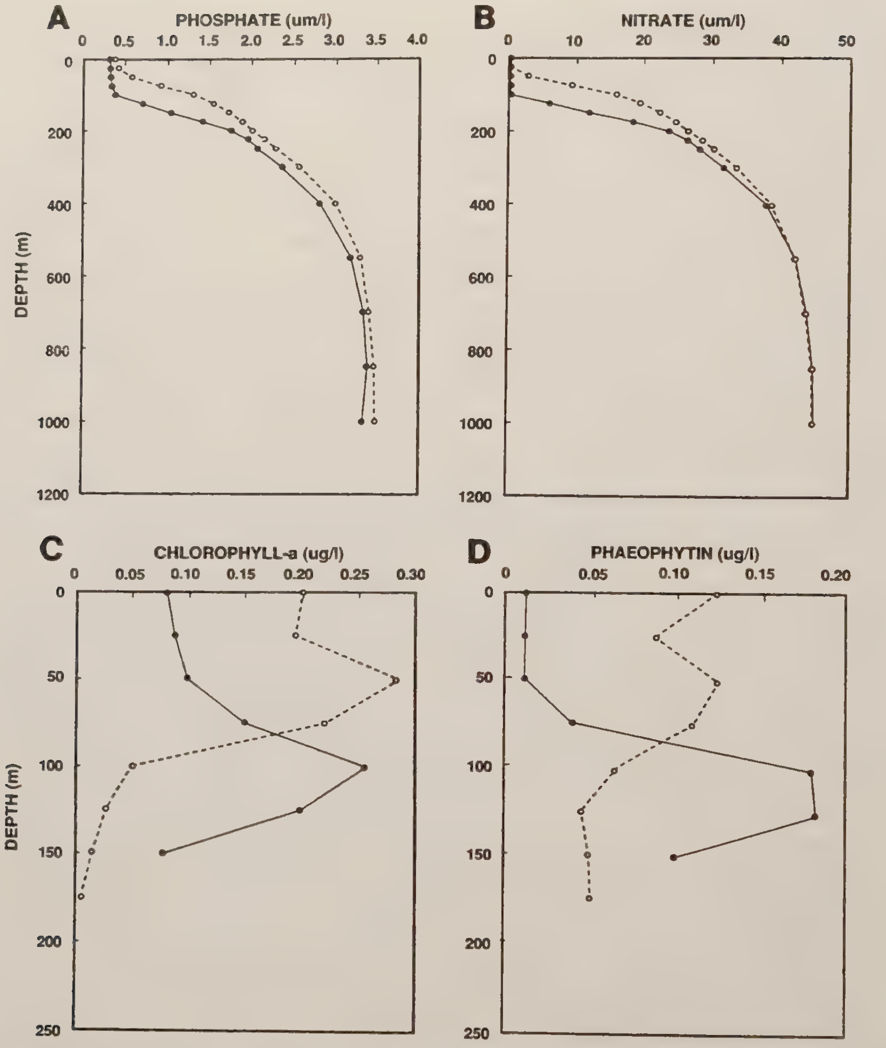

Figure 19. Depth profiles of concentrations of phosphate (A), nitrate (B), chlorophyll-*a* (C), and phaeophytin (D) for Station 2, Cast 8 at the southern end of the FRONTS 85 transect (closed circles) and for Station 10, Cast 1 at the northern end (open circles). Data from Haury et al. (1986).

1980; Ahlstrom, 1972a) and some of these taxa are important constituents of the Southern Complex of assemblages in the CalCOFI survey area. The myctophids *C. townsendi* and *D. atlanticus* ranked third and sixth in total abundance in Loeb's (1980) Central Water Mass study and formed the Southern Complex recurrent group DIOGENICHTHYS in the CalCOFI area. The myctophid *D. laternatus* and the phosichthyid *V. lucetia* ranked first and second in abundance in Ahlstrom's (1972a) ETP study and, with two myctophids, formed the Southern Complex recurrent group VINCIGUERRIA in our study.

In addition to those recurrent groups that are clearly associated with distinct

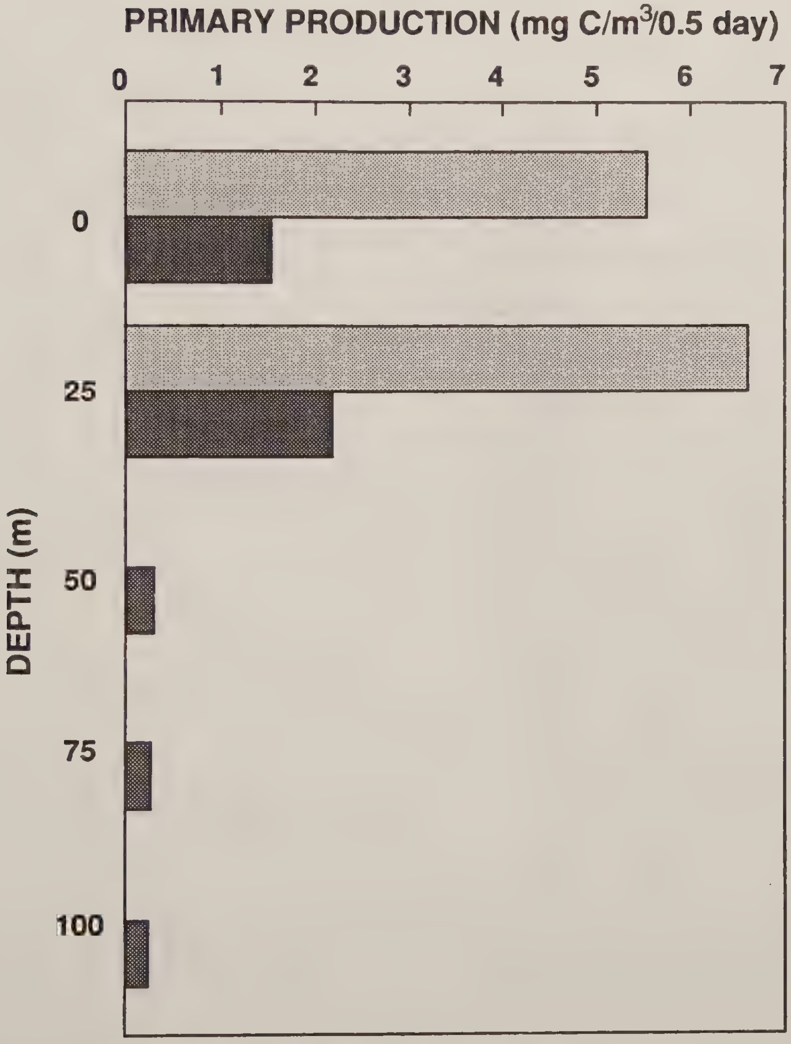

Figure 20. Primary production vs. depth derived from noon-to-dusk incubations at Station 2 at the southern end of the FRONTS 85 transect on June 13, 1985 (dark bars) and at Station 10 at the northern end on June 16, 1984 (light bars). Data from Haury et al. (1986).

water masses, our analysis identified SYMBOLOPHORUS, the major group of the Southern Complex. All of its member taxa, except *Cyclothone* spp., have distributions of larvae that are centered in the California Current and extend southward to the warmer waters off central Baja California. The two species of *Cyclothone* that are well represented in CalCOFI, *C. acclinidens* and *C. signata,* are distributed across the equatorial Pacific and penetrate eastward into the southern half of the CalCOFI pattern. Their larvae have not been routinely identified in CalCOFI samples.

The CalCOFI survey area overlies two coastal faunal provinces, the Oregonian

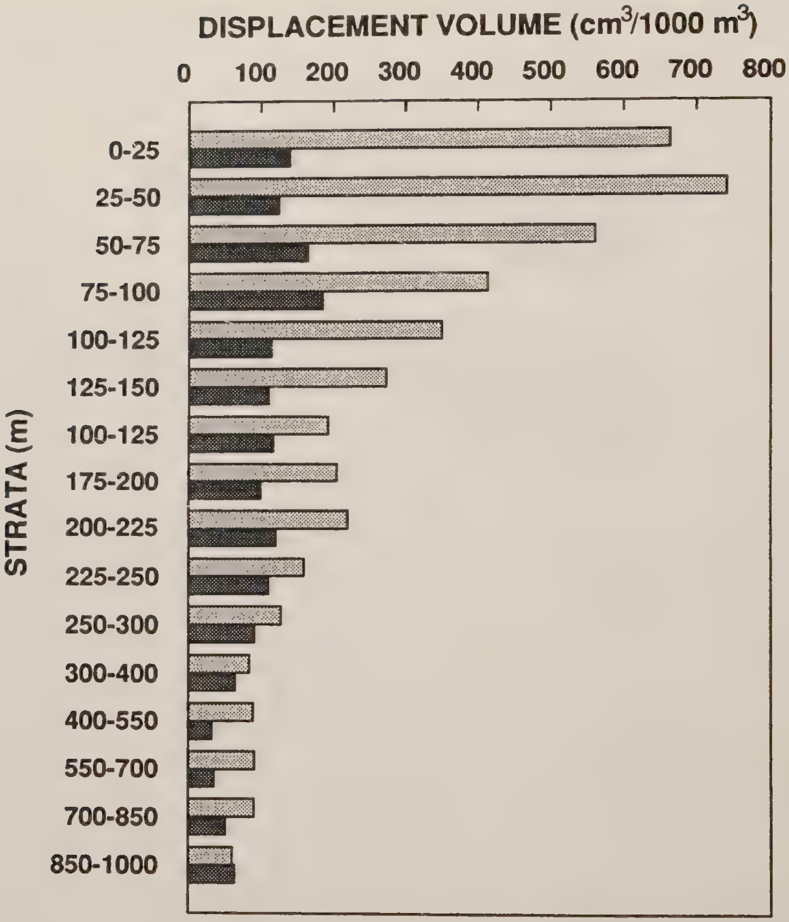

Figure 21. Mean zooplankton displacement volumes for stations at the southern end of the FRONTS 85 transect (dark bars) and for stations at the northern end (light bars). Data from Haury et al. (1986).

Province north of Point Conception and the San Diegan Province from Point Conception south to Magdalena Bay, Baja California (Allen and Smith, 1988). The Panamic Tropical Province south of Magdalena Bay was sampled on relatively few CalCOFI surveys during the 1950's. Annual and seasonal coverage off northern California was sporadic in the 1951–1984 period and the shelf was poorly sampled. Accordingly, our analysis did not identify the distinct coastal, shelf transition, and oceanic larval fish assemblages as described by Richardson et al. (1980) for Oregon and by Doyle et al. (this volume) for the Washington-Oregon-Northern California region.

The coastal environment off southern California is characterized by a narrow shelf, a circulation pattern dominated by the Southern California Eddy, and the topographically complex Southern California Borderland. Larvae of coastal taxa occur far offshore, especially coastal pelagics, while mesopelagic species occupy the borderland basins and impinge on the narrow shelf region. Despite this com-

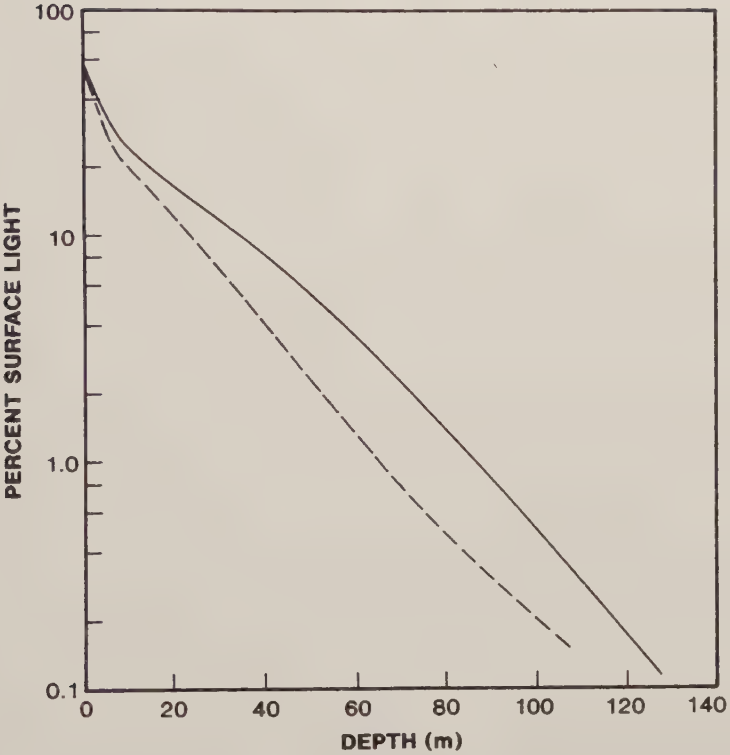

Figure 22. Light penetration (percent of surface light) at Station 2 at the southern end of the FRONTS 85 transect (solid line) and at Station 10 at the northern end (broken line). Data provided by L. R. Haury (Scripps Institution of Oceanography).

plexity, there is considerable overlap among larval fish assemblages described in regional studies of the Southern California Bight and those described for the more extensive CalCOFI survey area. The major recurrent group of Gruber et al. (1982) included three of the five members of our LEUROGLOSSUS group, with the other two members as associates. Another group identified by Gruber et al. (1982) was essentially the same as our PARALICHTHYS and a third group consisted of summer-spawning shelf taxa. A major assemblage in McGowen's (this volume) analysis of nearshore ichthyoplankton included three of our LEUROGLOSSUS taxa. Also, three of the five taxa of our SYNODUS recurrent group formed a distinct sub-unit in his large summer-spawning assemblage.

The only extensive shelf areas sampled thoroughly on CalCOFI surveys were Sebastian Viscaino Bay and the area between Point Eugenia and Cape San Lazaro, within the southern part of the San Diegan faunal province (Allen and Smith, 1988). SYNODUS, the only large nearshore recurrent group identified by the analysis, was centered in this area. Taxa in this group were not abundant enough to be included in the cluster or principal component analysis. Distributions of group members ranged northward to the Southern California Bight with minima along the cold, upwelling region of northern Baja California, characterized by its narrow shelf. The robust nature of the group is evident from its presence in the

Table 5. Larva-weighted mean values for depth, temperature, salinity, density, dissolved oxygen, chlorophyll-*a*, and zooplankton displacement volume for 10 larval fish taxa occurring in MOCNESS tows at the south and north ends of the FRONTS 85 transect

| | Depth (m) | | Temperature (°C) | | Salinity (ppt) | | Density ($kg \cdot m^{-3}$) | | Dissolved $O_2$ ($ml \cdot liter^{-1}$) | | Chlorophyll-*a* ($mg \cdot m^{-3}$) | | Zooplankton ($cm^3 \cdot 1{,}000\ m^{-3}$) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | S | N | S | N | S | N | S | N | S | N | S | N | S | N |
| Northern Complex | | | | | | | | | | | | | | |
| TARLETONBEANIA | | | | | | | | | | | | | | |
| *Diaphus* spp. | 109 | 62 | 12.91 | 12.21 | 33.47 | 33.39 | 25.20 | 25.29 | 5.18 | 5.56 | 0.14 | 0.24 | 168 | 572 |
| Southern Complex | | | | | | | | | | | | | | |
| SYMBOLOPHORUS | | | | | | | | | | | | | | |
| *Trachurus symmetricus* | 48 | 41 | 15.92 | 13.59 | 33.39 | 33.29 | 24.51 | 24.94 | 5.87 | 5.98 | 0.12 | 0.26 | 142 | 710 |
| *Bathylagus wesethi* | 151 | 82 | 11.01 | 11.32 | 33.59 | 33.46 | 25.67 | 25.52 | 4.46 | 5.09 | 0.09 | 0.17 | 107 | 417 |
| *Symbolophorus californiensis* | 161 | 99 | 10.79 | 11.09 | 33.64 | 33.54 | 25.74 | 25.61 | 4.24 | 4.78 | 0.09 | 0.15 | 119 | 458 |
| *Melamphaes* spp. | 175 | 148 | 10.31 | 9.63 | 33.73 | 33.75 | 25.89 | 26.03 | 3.83 | 3.77 | 0.03 | 0.05 | 107 | 240 |
| *Lestidiops ringens* | 185 | 72 | 9.50 | 11.85 | 33.80 | 33.42 | 26.10 | 25.39 | 3.48 | 5.32 | 0.01 | 0.20 | 106 | 559 |
| *Protomyctophum crockeri* | 335 | 253 | 7.19 | 7.72 | 34.07 | 34.02 | 26.66 | 26.54 | 1.91 | 2.45 | — | — | 66 | 180 |
| *Microstoma microstoma* | 387 | 323 | 7.20 | 7.28 | 34.05 | 34.09 | 26.63 | 26.67 | 1.98 | 2.01 | — | — | 78 | 167 |
| TRIPHOTURUS | | | | | | | | | | | | | | |
| *Triphoturus mexicanus* | 85 | 58 | 13.87 | 12.79 | 33.37 | 33.36 | 24.94 | 25.15 | 5.67 | 5.62 | 0.16 | 0.22 | 157 | 673 |
| *Lampanyctus* spp. | 179 | 75 | 10.24 | 11.79 | 33.72 | 33.46 | 25.90 | 25.41 | 3.91 | 5.16 | 0.06 | 0.18 | 112 | 532 |

analysis of the 1954–1960 subset of the CalCOFI time series and in individual years in that subset (Moser et al., 1987). The strong northward flowing countercurrent located off the shelf edge along Baja California probably plays an important role in supplying larvae of these warm water taxa to the Southern California Bight.

The spacing of the CalCOFI sampling grid is adequate to define distributions of larval fish taxa and the structure of assemblages; however, definition of distributions at frontal boundaries requires fine scale, three-dimensional sampling in conjunction with satellite imaging. This is clearly shown by the new information reported here on larval fish distributions at the Ensenada Front. Although the south-north transect of the cruise was only 120 n. mi. long, the change from the southern to the northern CalCOFI larval fish complexes was apparent. This was most clearly demonstrated for the Northern Complex by *T. crenularis* (TARLETONBEANIA recurrent group) whose larvae were absent from MOCNESS tows at the southern station and from bongo tows on all stations south of mid-transect. *Diaphus* spp., an affiliate of TARLETONBEANIA, was 15 times more abundant in MOCNESS tows at the northern MOCNESS station compared with the south. LEUROGLOSSUS, the major Northern Complex group, was poorly represented on the FRONTS 85 cruise because its members are primarily winter-spring spawners; however, those that were present on FRONTS 85 (*B. ochotensis, L. stilbius, S. leucopsarus, Sebastes* spp.) occurred only in northern MOCNESS samples and in bongo samples from the northern part of the transect. Definitive information on the distribution these species at the front awaits sampling of the front during winter or spring; thus far, all cruises have been in the summer when the front is most strongly developed (Niiler et al., 1989).

Distributional boundaries of most Southern Complex taxa were less clearly defined than those of the Northern Complex on the FRONTS 85 cruise; however, taxa with affinities to equatorial or central gyre water showed a clear pattern. *V. lucetia* (VINCIGUERRIA) and *C. townsendi* (CERATOSCOPELUS) were present only in tows from the southern MOCNESS station and showed a marked decline in mean abundance in bongo tows in the northern part of the transect. *Cyclothone* spp. (SYMBOLOPHORUS) had a similar pattern except for a single occurrence in a MOCNESS sample from the northern station. Most members of SYMBOLOPHORUS had greater numbers of occurrences at the southern MOCNESS station compared with the northern station even though abundance showed no clear south-north pattern. In bongo tows, some SYMBOLOPHORUS taxa (*B. wesethi, P. crockeri, T. symmetricus*) showed abundance peaks at mid-transect stations where gradients of physical properties were greatest, while *S. californiensis* had lower mean abundance at mid-transect stations.

The MOCNESS samples showed that vertical distributions of larval fish taxa on the north side of the front were shallower than on the south side. This is true for *Diaphus* spp., the only taxon of the Northern Complex occurring at both north and south MOCNESS stations in sufficient abundance to show a pattern. Members of SYMBOLOPHORUS shoaled to varying degrees at the northern station. For some species (*T. symmetricus* and *S. californiensis*) the overall vertical ranges did not change but the modal peak shifted. In other taxa (*B. wesethi* and *P. crockeri*) the upward shift of distributions at the northern station was more pronounced and there was only partial overlap of the distributions at the two stations. The most striking difference occurred in a SYMBOLOPHORUS affiliate, *L. ringens,* whose larvae had non-overlapping distributions at the two stations with peaks separated by a depth interval of 100 m. In another affiliate of the group, *M. microstoma,* the northern and southern peaks were at 200–225 m and 300–400 m, respectively, showing that the shoaling effect occurred deep in the water column. Shoaling at the northern station also occurred in TRIPHOTURUS, the other Southern Complex group whose member taxa (*T. mexicanus* and *Lampanyctus* spp.) occurred at the northern and southern stations.

Typically, major recurrent groups are composed of taxa whose larvae occupy a variety of depth strata. For example, LEUROGLOSSUS contains some taxa with relatively shallow distributions, *Sebastes* spp. and *S. leucopsarus,* and some with deeper depth profiles, *L. stilbius, B. ochotensis* and *M. productus* (Fig. 11; Ahlstrom, 1959; Moser and Boehlert, 1991). In SYMBOLOPHORUS, larvae of *T. symmetricus* are shallow living, *Cyclothone* spp. and *L. ritteri* have moderately shallow distributions, larvae of *B. wesethi* and *P. crockeri* are moderately deep, and *S. californiensis* are widely distributed in the water column (Figs. 13, 14; Ahlstrom, 1959). In VINCIGUERRIA, *V. lucetia* larvae are shallow living, while those of *D. laternatus, G. tenuiculus,* and *H. atratum* are moderately deep (Fig. 15; Loeb and Nichols, 1984). The two members of CERATOSCOPELUS have contrasting vertical distributions; *C. townsendi* is moderately shallow and *D. atlanticus* moderately deep (Fig. 15). This diversity in vertical distribution within groups may reflect adaptation of larvae of these taxa to environmental variables in different depth strata and is, at least, suggestive that vertical habitat diversity and resource partitioning may play a role in the structure of larval fish assemblages. Concentrations of larval fish prey vary with depth and are generally higher in the surface waters. For example, Beers and Stewart (1969, 1971) found maximum concentrations of 0.035- to 0.202-mm zooplankters in the upper 70 m of the water column at a variety of locales in the tropical and temperate eastern Pacific. The vertical ranges of larvae of the highly abundant coastal pelagic (*E. mordax, S. sagax, T. symmetricus, S. japonicus*) and mesopelagic (*V. lucetia, Cyclothone* spp.) fishes of this region also occupy this stratum (Figs. 12–15; Ahlstrom, 1959). The same or closely related coastal pelagic species occur in all eastern boundary currents (Bakun, 1985) and their larvae are a dominant fraction of the ichthyoplankton of these regions (Santander and Flores, 1983; Loeb and Rojas, 1988; Olivar and Shelton, this volume). It is likely that shallow distributions, centered in the zone of highest primary production and zooplankton biomass, are a requirement for their high larval production. There, survival may be enhanced by higher light intensity leading to more visible prey and by higher temperatures and concomitant higher metabolic and growth rates. This is balanced by increased mortality from probable increased predation rates. We suggest that species with lower production of larvae, living in deeper strata, experience conditions opposite to those listed above. Lower production of larvae is balanced by physiological and behavioral adaptations to diminished prey concentrations and by reduced predation pressure.

The apparent interaction of trophic dynamics and larval vertical distribution is particularly striking in the Myctophidae. The lanternfish subfamily Myctophinae (e.g., *T. crenularis, S. californiensis, P. crockeri, D. atlanticus*) have deeper distributions than larvae of the other major subfamily, the Lampanyctinae (e.g., *S. leucopsarus, Diaphus* spp., *C. townsendi, Lampanyctus* spp., *T. mexicanus*). The opposite is true for the adults of the two subfamilies, since adult myctophines are comparatively shallow living strong vertical migrators, while adult lampanyctines are deeper living and may or may not undergo diurnal vertical migrations (Clarke, 1973; Wisner, 1976; Loeb, 1986). Thus, the larval and adult stages of each subfamily are effectively separated vertically as Ahlstrom (1959) and Loeb (1980, 1986) have pointed out. We suggest that this pattern of vertical separation would limit the encounters between larvae and adults of the same species and may have evolved through selection for reduced mortality from cannibalism.

The shift to shallower distributions for larvae in the north is mirrored by environmental features. Isopleths of temperature, salinity, density, dissolved oxygen, and nutrients shoal from south to north along the transect. The abrupt change of isotherms and isohalines at the middle of the transect indicates a strong frontal feature. At the northernmost station, primary productivity is more than double that at the southernmost station and zooplankton standing stock is three times larger at the northern station. As with physical properties, the change in productivity and zooplankton biomass is greatest at mid-transect (Haury et al., 1993). Depth of the chlorophyll maximum is at 50 m in the north and at 100 m in the south. Changes in vertical distribution of larval fish taxa may be related to one or more of these parameters; however, larva-weighted mean values of physical properties at the northern and southern station indicated that larvae did not maintain a constant environment by changing their depth distribution. It is unlikely that deeper distributions at the southern station are related to subduction of northern surface waters south of the front, since changes in vertical distribution occurred in all species regardless of their position in the water column. Lack of vertically discrete samples from other than the terminal stations on the transect precluded further examination of this hypothesis. We suggest that changes in vertical distribution of larvae are most likely related to changes in trophic conditions and larval shoaling may involve an interplay of the vertical shift of maximum prey densities and specific feeding behaviors that are light-level dependent. Diel changes in the vertical distribution of herring (*Clupea harengus*) larvae provide inferential support for this hypothesis (Munk et al., 1989). In the daytime, herring larvae occupied depths where light was sufficient for feeding and vertical adjustments in that zone were apparently a compromise between optimal light conditions for feeding and optimal prey densities. Extension of these findings to explain changes in vertical distribution of larval fish assemblages across the Ensenada Front will require synoptic vertical profiling of fish larvae, microzooplankton, and irradiance.

The discovery that many California Current species have deep living larvae has important implications in the interpretation of CalCOFI data. Some of these larval fish distributions are below the 210-m depth for standard tows and many are below 140 m, the standard tow depth on surveys during 1951 to 1968. Calculations of abundance based on numbers of larvae per unit surface area would be variously underestimated for many species. Indeed, one wonders how some of the very deep living taxa (e.g., *M. microstoma, Argyropelecus* spp., *D. oculatus*) ever occur in CalCOFI tows. Standard tow depths encompass the vertical ranges of larvae of the principal CalCOFI target species (clupeioids and other coastal pelagics); however, studies of community dynamics would require deeper tows to sample the entire larval ichthyofauna quantitatively.

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Appendix. Composition of larval fish recurrent groups and their associate and affiliate taxa from CalCOFI survey data, 1951 to 1984. Associates listed under each recurrent group may include members or associates of other recurrent groups

| Taxon | Incidence (of 31,214) | Associate group |
|---|---|---|
| Northern Complex | | |
| LEUROGLOSSUS | | |
| *Sebastes* spp. | 12,322 | |
| *Leuroglossus stilbius* | 8,509 | |
| *Merluccius productus* | 7,372 | |
| *Stenobrachius leucopsarus* | 7,258 | |
| *Bathylagus ochotensis* | 4,555 | |
| Associates | | |
| *Engraulis mordax* | 14,486 | CITHARICHTHYS |
| *Protomyctophum crockeri* | 8,048 | SYMBOLOPHORUS |
| *Citharichthys* spp. | 6,322 | CITHARICHTHYS |
| *Tarletonbeania crenularis* | 4,041 | TARLETONBEANIA |
| *Icichthys lockingtoni* | 1,992 | TARLETONBEANIA |
| Affiliates | | |
| *Argentina sialis* | 1,294 | |
| *Tetragonurus cuvieri* | 1,031 | |
| Chiasmodontidae | 726 | |
| *Bathylagus* spp. | 676 | |
| *Bathylagus pacificus* | 536 | |
| *Sebastolobus* spp. | 462 | |
| *Sebastes paucispinis* | 372 | |
| *Sebastes jordani* | 209 | |
| *Brosmophycis marginata* | 208 | |
| *Zaniolepis* spp. | 207 | |
| *Scorpaenichthys marmoratus* | 206 | |
| *Brama* spp. | 166 | |
| *Medialuna californiensis* | 152 | |
| *Oxylebius pictus* | 147 | |
| Macrouridae | 137 | |
| *Bathylagus milleri* | 106 | |
| Gempylidae | 101 | |
| *Sebastes aurora* | 91 | |
| *Sebastes levis* | 44 | |
| *Icosteus aenigmaticus* | 40 | |
| Hexagrammidae | 37 | |
| Carapidae | 19 | |
| Osmeridae | 13 | |
| *Ophiodon elongatus* | 13 | |
| Uranoscopidae | 7 | |
| *Anoplopoma fimbria* | 5 | |
| Merlucciidae | 1 | |

Appendix. Continued

| Taxon | Incidence (of 31,214) | Associate group |
|---|---|---|
| TARLETONBEANIA | | |
| *Tarletonbeania crenularis* | 4,041 | |
| *Icichthys lockingtoni* | 1,992 | |
| Associates | | |
| *Sebastes* spp. | 12,322 | LEUROGLOSSUS |
| *Leuroglossus stilbius* | 8,509 | LEUROGLOSSUS |
| *Stenobrachius leucopsarus* | 7,258 | LEUROGLOSSUS |
| *Bathylagus ochotensis* | 4,555 | LEUROGLOSSUS |
| Affiliates | | |
| *Diaphus* spp. | 2,118 | |
| *Chauliodus macouni* | 1,701 | |
| Trachipteridae | 650 | |
| *Protomyctophum thompsoni* | 23 | |
| *Leuroglossus schmidti* | 3 | |
| *Parvilux ingens* | 3 | |
| *Dolichopteryx longipes* | 1 | |
| SARDINOPS | | |
| *Sardinops sagax* | 2,999 | |
| *Scomber japonicus* | 1,211 | |
| Associates | | |
| *Engraulis mordax* | 14,486 | CITHARICHTHYS |
| Affiliates | | |
| *Sphyraena argentea* | 301 | |
| *Euthynnus* spp. | 4 | |
| CITHARICHTHYS | | |
| *Engraulis mordax* | 14,486 | |
| *Citharichthys* spp. | 6,322 | |
| Associates | | |
| *Sebastes* spp. | 12,322 | LEUROGLOSSUS |
| *Triphoturus mexicanus* | 11,968 | TRIPHOTURUS |
| *Leuroglossus stilbius* | 8,509 | LEUROGLOSSUS |
| *Merluccius productus* | 7,732 | LEUROGLOSSUS |
| *Stenobrachius leucopsarus* | 7,258 | LEUROGLOSSUS |
| *Sardinops sagax* | 2,999 | SARDINOPS |
| Sciaenidae | 1,973 | PARALICHTHYS |
| Affiliates | | |
| Gobiidae | 1,991 | |
| *Peprilus simillimus* | 713 | |
| *Oxyjulis californica* | 467 | |
| Pleuronectiformes | 217 | |
| Cyclopteridae | 203 | |
| *Sygnathus* spp. | 154 | |
| *Sarda chiliensis* | 123 | |
| *Girella nigricans* | 73 | |
| *Macroramphosus gracilis* | 71 | |
| *Sebastes macdonaldi* | 63 | |
| Blennioidei | 62 | |
| Gobiesocidae | 60 | |
| *Physiculus* spp. | 42 | |
| *Lepidopus xantusi* | 39 | |
| *Hypsypops rubicundus* | 16 | |
| *Cubiceps pauciradiatus* | 12 | |

Appendix. Continued

| Taxon | Incidence (of 31,214) | Associate group |
|---|---|---|
| *Porichthys* spp. | 12 | |
| *Microgadus proximus* | 9 | |
| Alepocephalidae | 3 | |
| *Gadus macrocephalus* | 1 | |
| CITHARICHTHYS A | | |
| *Citharichthys xanthostigma* | 984 | |
| *Citharichthys fragilis* | 821 | |
| Affiliates | | |
| *Citharichthys stigmaeus* | 2,710 | |
| *Citharichthys sordidus* | 450 | |
| *Caulolatilus princeps* | 89 | |
| *Seriola* spp. | 3 | |
| *Anotopterus pharao* | 3 | |
| PARALICHTHYS | | |
| Sciaenidae | 1,973 | |
| *Paralichthys californicus* | 1,105 | |
| Associates | | |
| *Engraulis mordax* | 14,486 | CITHARICHTHYS |
| Affiliates | | |
| Cottidae | 722 | |
| Clinidae | 600 | |
| Agonidae | 247 | |
| Atherinidae | 125 | |
| *Genyonemus lineatus* | 104 | |
| *Seriphus politus* | 31 | |
| Acanthuridae | 1 | |
| Southern Complex | | |
| SYMBOLOPHORUS | | |
| *Protomyctophum crockeri* | 8,048 | |
| *Cyclothone* spp. | 5,869 | |
| *Trachurus symmetricus* | 5,612 | |
| *Bathylagus wesethi* | 5,593 | |
| *Lampanyctus ritteri* | 4,707 | |
| *Symbolophorus californiensis* | 3,219 | |
| Associates | | |
| *Triphoturus mexicanus* | 11,968 | TRIPHOTURUS |
| *Vinciguerria lucetia* | 10,510 | VINCIGUERRIA |
| *Leuroglossus stilbius* | 8,509 | LEUROGLOSSUS |
| *Stenobrachius leucopsarus* | 7,258 | LEUROGLOSSUS |
| *Lampanyctus* spp. | 5,841 | TRIPHOTURUS |
| *Diogenichthys laternatus* | 5,043 | VINCIGUERRIA |
| *Bathylagus ochotensis* | 4,555 | LEUROGLOSSUS |
| *Melamphaes* spp. | 4,065 | |
| Myctophidae | 3,806 | VINCIGUERRIA |
| *Ceratoscopelus townsendi* | 3,058 | CERATOSCOPELUS |
| *Diogenichthys atlanticus* | 2,706 | CERATOSCOPELUS |
| *Stomias atriventer* | 2,548 | VINCIGUERRIA |
| Affiliates | | |
| Sternoptychidae | 2,934 | |
| Paralepididae | 1,334 | |
| *Lestidiops ringens* | 1,210 | |
| Scopelarchidae | 944 | |

Appendix. Continued

| Taxon | Incidence (of 31,214) | Associate group |
|---|---|---|
| *Microstoma microstoma* | 681 | |
| *Cololabis saira* | 513 | |
| *Lampanyctus regalis* | 455 | |
| *Poromitra* spp. | 452 | |
| *Scopelogadus bispinosus* | 434 | |
| *Nansenia candida* | 431 | |
| *Danaphos oculatus* | 218 | |
| *Notolepis risso* | 136 | |
| *Tactostoma macropus* | 121 | |
| *Electrona rissoi* | 115 | |
| *Scopelarchus* spp. | 102 | |
| *Rosenblattichthys volucris* | 88 | |
| *Stemonosudus macrura* | 28 | |
| *Scopeloberyx robustus* | 27 | |
| *Benthalbella dentata* | 27 | |
| Evermannellidae | 19 | |
| *Sudis atrox* | 17 | |
| Apogonidae | 16 | |
| Eutaeniophoridae | 9 | |
| *Triphoturus nigrescens* | 7 | |
| Myctophiformes | 4 | |
| *Gonostoma* spp. | 3 | |
| *Hygophum proximum* | 2 | |
| *Bathylychnops exilis* | 1 | |
| VINCIGUERRIA | | |
| *Vinciguerria lucetia* | 10,510 | |
| *Diogenichthys laternatus* | 5,043 | |
| *Hygophum atratum* | 1,309 | |
| *Gonichthys tenuiculus* | 1,234 | |
| Associates | | |
| *Triphoturus mexicanus* | 11,968 | TRIPHOTURUS |
| *Protomyctophum crockeri* | 8,048 | SYMBOLOPHORUS |
| *Cyclothone* spp. | 5,869 | SYMBOLOPHORUS |
| *Lampanyctus* spp. | 5,841 | TRIPHOTURUS |
| *Bathylagus wesethi* | 5,593 | SYMBOLOPHORUS |
| Myctophidae | 3,806 | SYMBOLOPHORUS |
| *Ceratoscopelus townsendi* | 3,058 | CERATOSCOPELUS |
| *Stomias atriventer* | 2,548 | SYMBOLOPHORUS |
| Affiliates | | |
| *Nansenia crassa* | 836 | |
| *Ichthyococcus* spp. | 426 | |
| Astronesthidae | 3 | |
| *Macropinna microstoma* | 3 | |
| *Oxyporhamphus micropterus* | 1 | |
| TRIPHOTURUS | | |
| *Triphoturus mexicanus* | 11,968 | |
| *Lampanyctus* spp. | 5,481 | |
| Associates | | |
| *Engraulis mordax* | 14,486 | CITHARICHTHYS |
| *Vinciguerria lucetia* | 10,510 | VINCIGUERRIA |
| *Protomyctophum crockeri* | 8,048 | SYMBOLOPHORUS |
| *Cyclothone* spp. | 5,869 | SYMBOLOPHORUS |
| *Trachurus symmetricus* | 5,612 | SYMBOLOPHORUS |
| *Bathylagus wesethi* | 5,593 | SYMBOLOPHORUS |
| *Diogenichthys laternatus* | 5,043 | VINCIGUERRIA |

Appendix. Continued

| Taxon | Incidence (of 31,214) | Associate group |
|---|---|---|
| Myctophidae | 3,806 | SYMBOLOPHORUS |
| *Ceratoscopelus townsendi* | 3,058 | CERATOSCOPELUS |
| Affiliates | | |
| *Diogenichthys* spp. | 909 | |
| *Hygophum* spp. | 408 | |
| Gonostomatidae | 271 | |
| *Loweina rara* | 224 | |
| Stomiiformes | 143 | |
| Exocoetidae | 73 | |
| CERATOSCOPELUS | | |
| *Ceratoscopelus townsendi* | 3,058 | |
| *Diogenichthys atlanticus* | 2,706 | |
| Associates | | |
| *Vinciguerria lucetia* | 10,510 | VINCIGUERRIA |
| *Protomyctophum crockeri* | 8,048 | SYMBOLOPHORUS |
| *Cyclothone* spp. | 5,869 | SYMBOLOPHORUS |
| *Bathylagus wesethi* | 5,593 | SYMBOLOPHORUS |
| *Symbolophorus californiensis* | 3,219 | SYMBOLOPHORUS |
| *Lampadena urophaos* | 722 | |
| *Notoscopelus resplendens* | 674 | |
| Affiliates | | |
| *Idiacanthus antrostomus* | 843 | |
| *Myctophum nitidulum* | 795 | |
| *Lampadena urophaos* | 722 | |
| *Hygophum reinhardtii* | 414 | |
| *Notolychnus valdiviae* | 238 | |
| *Scopelosaurus* spp. | 236 | |
| *Aristostomias scintillans* | 196 | |
| *Bathophilus* spp. | 104 | |
| *Vinciguerria poweriae* | 63 | |
| *Photonectes* spp. | 34 | |
| *Centrobranchus* spp. | 26 | |
| *Valenciennellus stellatus* | 16 | |
| *Eustomias* spp. | 7 | |
| *Bathylagus longirostris* | 6 | |
| *Woodsia nonsuchae* | 1 | |
| *Taaningichthys minimus* | 1 | |
| *Lobianchia* spp. | 1 | |
| Southern Coastal Complex | | |
| SYNODUS | | |
| *Symphurus* spp. | 1,038 | |
| *Synodus* spp. | 1,008 | |
| *Ophidion scrippsae* | 502 | |
| *Etrumeus teres* | 437 | |
| *Prionotus* spp. | 363 | |
| Associates | | |
| Ophidiiformes | 847 | |
| Serranidae | 759 | |
| Carangidae | 211 | |
| Affiliates | | |
| *Lyopsetta exilis* | 1,206 | |
| *Parophrys vetulus* | 953 | |
| Labridae | 931 | |

Appendix. Continued

| Taxon | Incidence (of 31,214) | Associate group |
|---|---|---|
| *Hypsoblennius* spp. | 910 | |
| *Pleuronichthys verticalis* | 893 | |
| *Hippoglossina stomata* | 756 | |
| Trichiuridae | 547 | |
| *Chromis punctipinnis* | 537 | |
| *Microstomus pacificus* | 479 | |
| Anguilliformes | 386 | |
| *Chilara taylori* | 306 | |
| *Scorpaena* spp. | 305 | |
| *Glyptocephalus zachirus* | 276 | |
| *Halichoeres* spp. | 266 | |
| *Seriola lalandi* | 233 | |
| *Xystreurys liolepis* | 202 | |
| *Pleuronichthys* spp. | 181 | |
| *Pleuronichthys ritteri* | 165 | |
| *Pleuronichthys coenosus* | 157 | |
| Haemulidae | 134 | |
| *Semicossyphus pulcher* | 129 | |
| *Coryphaena hippurus* | 120 | |
| Gerreidae | 106 | |
| Pomacentridae | 104 | |
| *Bregmaceros* spp. | 101 | |
| *Auxis* spp. | 89 | |
| *Pleuronichthys decurrens* | 85 | |
| Scombridae | 84 | |
| *Etropus* spp. | 70 | |
| *Hypsopsetta guttulata* | 63 | |
| *Syacium ovale* | 48 | |
| *Bothus* spp. | 38 | |
| *Mugil* spp. | 29 | |
| *Opisthonema* spp. | 25 | |
| Nomeidae | 25 | |
| *Scomberomorus* spp. | 19 | |
| *Thunnus albacares* | 12 | |
| Hemiramphidae | 11 | |
| *Psenes pellucidus* | 11 | |
| Mullidae | 8 | |
| Tetraodontidae | 6 | |
| *Albula vulpes* | 5 | |
| Engraulidae | 5 | |
| *Hippoglossina* spp. | 3 | |
| Bothidae | 2 | |
| *Paralichthys* spp. | 2 | |
| Polynemidae | 2 | |
| *Cheilotrema saturnum* | 2 | |
| Priacanthidae | 1 | |
| *Roncador stearnsii* | 1 | |
| MICRODESMIDAE | | |
| Microdesmidae | 1 | |
| *Cyclopsetta* spp. | 1 | |
| Affiliates | | |
| Scorpaenidae | 34 | |
| *Benthosema pterota* | 12 | |
| *Aulopus* spp. | 11 | |
| PSENES | | |
| *Cubiceps pauciradiatus* | 12 | |
| *Psenes sio* | 5 | |

Appendix. Continued

| Taxon | Incidence (of 31,214) | Associate group |
|---|---|---|
| Affiliates | | |
| *Diplophos taenia* | 192 | |
| *Myctophum aurolaternatum* | 57 | |
| *Scopelarchoides nicholsi* | 19 | |
| SPARIDAE | | |
| Sparidae | 1 | |
| *Chaetodipterus zonatus* | 1 | |
| BALISTIDAE | | |
| Balistidae | 2 | |
| Fistulariidae | 1 | |

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# Guam's Small-Boat-based Fisheries

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*ABSTRACT—Recent trends in Guam's small-boat fisheries and current knowledge of their biology, management, and economics are summarized. Annual estimates of participation, effort, and harvest are given for the pelagic and bottomfish fisheries for 1980–91 and for the spearfishing and atulai fisheries for 1985. The pelagic fishery is the largest, with annual landings ranging from 168 to 364 metric tons (t), followed by the bottomfish fishery (14–43 t), spearfishing fishery (5–17 t), and bigeye scad fishery (3–20 t). All of the pelagic species are highly migratory and require regional management. They are heavily exploited by Guam-based domestic purse-seine and foreign longline fisheries, but region-wide catch and effort as well as the status of the stocks are largely unknown. Bottomfish and reef-fish stocks are shared to an unknown extent with those of the northern Marianas and are locally manageable. Certain vulnerable species of bottomfishes and reef fishes are overfished. Bottomfish and speared fish landings are dominated by small species with high turnover rates.*

## Introduction

Nearly 900 finfish species and a similar number of macroinvertebrate species inhabit the waters surrounding Guam. Approximately one-third of the species of finfishes and a smaller contingent of the invertebrates are utilized in the subsistence or commercial fisheries. Guam's exploited fisheries resources can be divided into the following five major groups based on biology and harvest method: Marine invertebrates, reef fishes, bottomfishes, pelagic fishes, and bigeye scad. Marine invertebrates include crustaceans, shelled mollusks, cephalopods, and echinoderms (Amesbury et al., 1986).

Echinoderms are generally harvested by reef gleaners and rarely with the aid of boats. Other invertebrates are harvested by hand or spear and with or without the use of boats. Reef fishes include all finfishes associated with coral reefs and adjacent sand flats and seagrass beds, as well as a small number of primarily estuarine species and are taken primarily by nets, spear, and hook and line with or without the use of boats.

Bottomfishes include reef fishes that occur beyond the seaward margin of the reef as well as deep-dwelling coastal fishes occuring to depths of approximately about 300 m that are taken by hook and line from boats. Pelagic fishes include migratory open-ocean species as well as a few coastal pelagic and reef species taken by lines trolled from a moving boat, longline, or ikashibi. The latter two methods have been rarely employed and are not currently in use. Nearly all pelagic landings consist of the following five species: Mahimahi, *Coryphaena hippurus*; wahoo, *Acanthocybium solandri*; skipjack tuna, *Katsuwonus pelamis*; yellowfin tuna, *Thunnus albacares*; and blue marlin, *Makaira mazara*. The bigeye scad, *Selar crumenophthalmus*, locally known as atulai, is a coastal pelagic species that undergoes seasonal migrations and is taken by a variety of methods from shore as well as from boats. Boats are used in coordination with a large number of shore-based snorkelers or scuba divers to set large nets around shallow inshore aggregations. The only offshore boat-based method used for this species is jigging at night with the aid of lights.

The original Chamoru inhabitants were expert fishermen and seafarers. Accounts by the early Spanish visitors indicate that they fished on the high seas for such formidable species as marlin and used numerous methods to catch reef and bottomfish from boats as well as from the shoreline (Amesbury et al., 1986). Throughout the Spanish period, the Chamorus were persecuted and an attempt was made to confine them to the island of Guam. Most of the male population was killed, and subsequent generations were of mixed blood. By the 1860's, there were only 24 outrigger canoes on Guam, all of which were used only for fishing inside the reef.

By the begining of the American period in 1898, the indigenous inhabitants had lost many of their seafaring and fishing skills as well as the native names of many of the offshore species. Small outboard and inboard powered boats did not become commonplace until after World War II. Fishing remained the primary motivation for boating, and the methods in use today were well established by the mid-1960's. Unlike many U.S. areas, the concept of fishing for sport is relatively new, and the use of "recreational-type" boating and fishing equipment and techniques for subsistence and commercial purposes is well established.

Trolling is the most popular and important fishing method and was employed on 85% of the boat trips during fiscal year 1991. Bottomfishing with hook and line using poles, handlines, or electric reels from either an anchored or a drifting boat was the second most important method. Spearfishing and jigging under a nightlight for bigeye scad followed in importance. Other rarely used methods include spincasting, longline, and ikashibi.

## Procedures

As presently designed, the offshore fisheries survey is a combined fixed-point and roving survey. For the fixed-point portion, personnel from Guam's Division of Aquatic and Wildlife Resources (DAWR) are stationed at one or more major boat landings during a given time-frame for a given number of days each month. All returning fishing parties are interviewed and, when possible, their catch is examined and samples measured or weighed. A log of all departing and returning fishing parties is also kept. The roving survey consists of a twice-a-day circuit in which all empty trailers attached to vehicles and the time of day are noted at each location. Information derived from the site log and the roving survey are used to calculate proportionality values based on the proportion of island-wide fishing activity occurring at the sampled site and the proportion of 24-hour fishing activity actually sampled at the sampled site. The proportionality values used to expand for site totals are method-specific, but those used to expand for island-wide totals are not, since the roving survey does not have the capability of obtaining information on methods. A set of standardized mathematical formulas is used by the Guam Offshore Expansion System (GOES), and its algorithms are used to expand sample-day totals into estimates of monthly, quarterly, and annual totals and their standard errors (SE) and confidence limits (CL). The GOES was prepared by CIC Research, Inc.[1], San Diego, Calif.) for the National Marine Fisheries Service (NMFS) and is available from the NMFS Honolulu Laboratory as Administrative Report H-83-21C. The inherent flexibility of GOES allows changes in sample periods, sites, and methods of determining proportionality constants in response to manpower or budgetary constraints as well as changes in the fisheries. The accuracy of the expansions is limited by the accuracy of the assumption that the sampled time-frames and sites are representative of the entire 24-hour period for the island as a whole. The precision of the expanded estimates is dependent on the sample size.

Prior to the implementation of the GOES, less reliable methods were used to estimate fishing activity from nonsampled sites. The original expansions assumed that activity from the sampled launch site, the Agana Boat Basin, was 50% of the island wide total. This was based on limited counts of boats using other launch sites during 1977–78. The expansions for 1977–82 were subsequently revised by using a set of proportionality figures based on observations made after implementation of the GOES. Surveys were initially limited to the hours of 0600 to 2100 or some portion within that time period. Fishing methods that occured at night were frequently undersampled. Therefore, in 1985 the survey period was divided into two shifts with the late shift extending as late as 2400 hours, and in 1986 it was further extended with the morning shift as early as 0500 hours. With implementation of a boating activity log, it became easier to track boats that could not be intercepted, allowing greater flexibility in the survey shift hours without compromising the comparability of results between years. Specific changes in methods, hours, or sites are detailed in annual reports produced by the DAWR.

The annual estimates of participation, effort, catch, and economics presented here were compiled from a combination of sources. The DAWR and NMFS each generate GOES output from the same data base on different, incompatible computer systems and have different reporting requirements. DAWR expands by gear and fiscal year (FY). NMFS expands by calendar year and by fishery, based on the species caught being categorized as either pelagic or bottomfish, and includes all methods for each of these respective species groups. Personnel, time, and hardware constraints made it impossible to generate standardized output for all parameters and methods. Annual estimates based on the sum of monthly expansions differ slightly from those based on a single period expansion. Annual CL and SE are known only for period expansions and are not presented herein. Whenever possible, information is presented in metric units by calendar year and method based on a period expansion. For some years and methods annual estimates are based on the sum of monthly expansions. All economic information is from annual summaries of commercial receipts compiled by NMFS. All annual estimates for trolling and bottomfishing are based on 362–day expansions (363 days in leap years) with landings from the annual 3-day Guam International Fishing Derby (GIFD) added in. Fishing by nonderby participants during the 3-day event is considered negligible. Annual estimates for spearfishing and night-lighting for atulai exclude the GIFD and are based on full monthly or annual expansions.

Summary data for the pelagic fishery are based entirely on NMFS output. In 1982 and 1985, only 1.7% and 0.2% of pelagic landings were by longline or ikashibi. An even smaller portion of the annual landings consists of sharks caught by other methods. Therefore, the pelagic fishery is considered synonymous with trolling since 98% or more of all annual landings are taken by this method.

Summaries of participation, effort, and catch data for the bottomfish fishery are based on DAWR expansions only and include all species caught by that method. Species composition is based on FY80–91 expansions. Economic summaries are based on NMFS data which exclude sharks and a small number of nonbottomfish species, but include bottomfish species caught by other methods. These differences are not considered large enough to affect the conclusions. Species composition for all other methods are based on fiscal year period expansions from October 1985 through September 1991.

## The Fisheries

### Pelagic Fishery

Guam's pelagic fishing fleet consists primarily of small recreational trolling boats that are either towed to

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[1] Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

launch sites or berthed in marinas. Presently most of vessels are <10 m long and are typically owner-operated by persons who earn a living outside of fishing. However, almost everyone sells a portion of their catch at one time or another, and it is impossible to make a distinction between recreational, subsistence, or commercial fishermen. A small but rapidly growing segment of the fleet are marina-berthed charter vessels that tend to be larger than the owner-operated vessels, ranging in length from 8 to >15 m. A small number of similar boats are operator or corporation-owned and are used for a variety of other recreational purposes as well as fishing.

### *The Catch*

Estimated overall pelagic landings have varied widely from year to year, ranging from a low of 168 metric tons (t) in 1987 to 364 t in 1991 (Fig. 1). A long-term trend is not detectable, but there does seem to be a slight general increase since 1987. Annual catches consist nearly entirely of five major species: Mahimahi, wahoo, skipjack tuna, yellowfin tuna, and Pacific blue marlin. Minor components include rainbow runner, *Elagatis bipinnulatus*; great barracuda, *Sphyraena barracuda*; kawakawa, *Euthynnus affinis*; dogtooth tuna, *Gymnosarda unicolor*; sailfish, *Istiophorus platypterus*; and shortbill spearfish, *Tetrapturus angustirostris*. Approximately a dozen additional species are landed incidentally each year.

Mahimahi landings exceeded those of all other species during 7 of the last 12 years, making it the single most important species of the pelagic fishery (Fig. 1). Annual landings ranged from 13 to 182 t, with no detectable trend or cycle. Mahimahi are seasonal, occurring during the winter and spring with a peak in March, although a few may be found throughout the year. More than any other species, the success of the mahimahi run determines whether it is a good or bad fishing year. No attempt has been made to compare catches from different western Pacific locations in a systematic manner. It remains unknown whether a good Guam run is the result of a healthy western Pacific year class or is due to vagaries of oceanographic conditions that concentrate the run near Guam.

Annual landings of wahoo ranged from 15 to 72 t. There is considerable variability from one year to the next with no apparent trends, and in only one year, 1985, did wahoo landings exceed those of all other species. Wahoo are caught throughout the year, but November is typically the best month. At that time, small wahoo of 2–4 kg are common. Most wahoo are immature, but mature fish in the 14–22 kg range are occasionally caught throughout the year. Wahoo are often caught relatively close to shore, and catches may increase during periods of high effort for mahimahi which may be in closer to shore during times of great abundance.

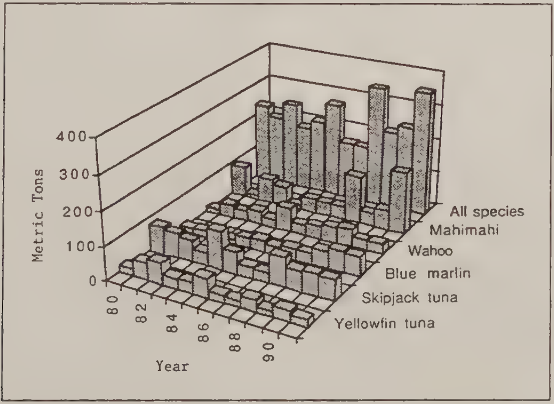

Figure 1.—Estimated annual landings of all pelagic fishes, mahimahi, wahoo, blue marlin, skipjack tuna, and yellowfin tuna by the Guam small-boat pelagic fishery during 1980–91.

Skipjack tuna is the second most important species with annual landings exceeding those of all others during 4 of the last 12 years. Landings are highly variable, ranging from 27 to 113 t (Fig. 1). Skipjack tuna occur in surface feeding schools throughout the year and are often the most easily caught fish, particularly when other species are scarce. However, the relatively low marketability of skipjack tuna makes them less desirable, so many boats do not target them and catches are probably poor indicators of relative abundance. The skipjack tuna caught by trolling near Guam are typically in the 2–6 kg range, but occasional fish weigh up to 9 kg. Skipjack tuna are heavily exploited by a large fleet of domestic purse seiners operating out of Guam. The effects of this exploitation on the stocks and the state of the stocks are unknown.

Annual yellowfin tuna landings were consistently lower than those of skipjack tuna, ranging from 16 to 62 t. Yellowfin tuna are highly valued, and relatively low catches are a reflection of low availability to surface trollers. Yellowfin tuna reach a large size (>160 kg), but most caught by local trollers are in the 2–20 kg range. Occasionally larger fish up to 70 kg are caught. Yellowfin tuna form the basis of the Guam-based foreign longline fishery and are of great importance to the domestic purse seine fishery. The effects of these fisheries on the availability of fish to the troll fishery as well as on the stocks themselves are unknown. Even if the yellowfin tuna stock is not overfished, interception of Guam-bound fish by the more efficient longliners and purse seiners could reduce their availability to the local trollers.

Annual blue marlin landings have increased significantly over the last 12 years, ranging from 15 t in 1980 to 62 t in 1990 (Fig. 1; $r^2 = 0.831$, $P<0.001$). In 1990, blue marlin landings exceeded those of all other species. The most rapid growth in landings occurred from 1988 to 1990. This is attributable to rapid growth of the charter fleet which tends to target blue marlin more often than the noncharter segment of the fleet. Blue marlin are seasonal; the best catches occur during the warmest months from June to September. Most of the troll-caught fish are small, <70 kg, and are males. Occasional blue marlin are caught throughout the year, including large females of 140–400 kg.

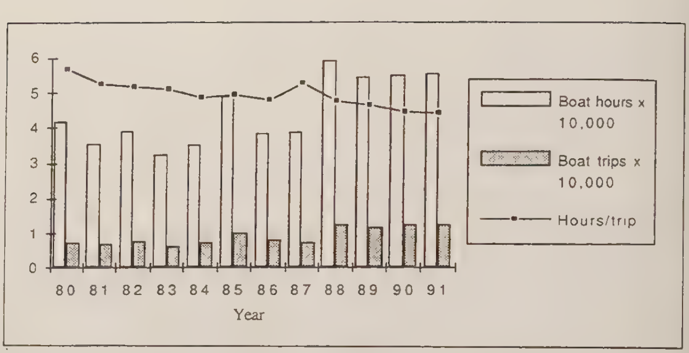

Figure 2.—Estimated annual number of boat trips, boat hours spent trolling, and hours spent trolling per boat trip around Guam during 1980–91.

### *Participation and Effort*

The exact number of boats or people participating in the troll fishery are unknown. The GOES enumerates boat-trips and person-trips. Therefore, a "threshold" C/E model is used by NMFS to estimate the annual number of boats participating in the fishery. The estimated number of boats increased more than twofold, from 115 to 282 between 1980 and 1989. The number has dropped somewhat since then, but more recent figures are considered low since the survey does not include boats that fish exclusively from unsampled sites which include a new marina that opened in early 1991. The increase in the number of boats over the 12–year period is significant ($r^2$ = 0.637, P<0.01)

The estimated annual number of boat trips ranged from 6,287 in 1981 to 12,523 in 1991; most of the increase ocurred after 1987 (Fig. 2). The number of boat hours spent trolling also increased significantly during the past 12 years ($r^2$ = 0.555, P<0.01), reaching a peak of nearly 59,000 in 1988. However, the number of hours per trip has decreased in recent years because of the increasing proportion of charter trips ($r^2$ = 0.775, P<0.001). Charter vessels typically carry more people but engage in shorter fishing trips than noncharter vessels.

### *Catch Rates*

Catch rates as catch per unit of effort (CPUE) are calculated by dividing the total annual landings of each species by the total number of boat-hours spent fishing (gear in use). Since it is impossible to allocate species-specific effort, catch rates for a given species calculated in this manner may be influenced by effort targeted towards other species. Catch rates for mahimahi and wahoo fluctuated widely over the past 12 years with no apparent trend (Fig. 3). Catch rates for skipjack tuna show a general decline with the exception of a sharp peak in 1984, and catch rates for yellowfin tuna declined significantly during the past 12 years ($r^2$ = 0.408, P<0.05). Catch rates for blue marlin increased significantly over the past 12 years ($r^2$ = 0.722, P<0.001). This is probably a result of the changing composition of the fleet toward more boats that are larger and better equipped to target and catch blue marlin. Recent low catch rates for skipjack tuna are likely due to economic reasons since that species is relatively unmarketable and many boats do not target it. The decline in catch rates for yellowfin tuna cannot be attributed to economic reasons since that species is highly valued and often targeted. When other factors are considered such as declining average and winning sizes at an annual fishing derby, it seems plausible that the reasons for the decline are related to the species' availability. Lower availability of yellowfin tuna, particulary the larger size classes, could be a result of either changes in the stock or of interception by competing fisheries.

### *Economics*

Guam's small-boat trolling fishery consists of recreational, subsistence,

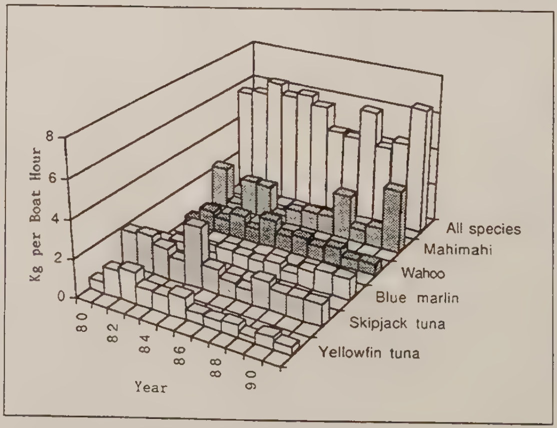

Figure 3.—Catch rates as kg per boat hour spent fishing for all pelagic fishes, mahimahi, wahoo, blue marlin, skipjack tuna, and yellowfin tuna by the Guam small-boat pelagic fishery during 1980–91.

and commercial fishermen, many of whom also engage in other methods of fishing. Most charter boat captains and crew are not employed elsewhere, but most other fishermen hold nonfishing jobs. Charter boat captains and crew generally supplement their pay with tips and proceeds from the sale of the day's catch. Many noncharter fishermen occasionally sell part of their catch, while a minority regularly sell all or most of their catch.

Over the past 12 years, an estimated 42% of the pelagic fish harvest was sold, generating inflation-adjusted annual revenues ranging from $340,532 to $635,006 (Fig. 4). The economics of Guam's trolling fishery is complex and has undergone numerous changes during the past 12 years. Inflation-adjusted revenue per trip has declined by 54% since 1983 (Fig. 5; $r^2 = 0.868$, $P<0.001$). This is due to a number of factors including loss of markets, when there is inadequate availability, inability to efficiently process and freeze or export fish when there is a glut, and competition from other sources that either import inexpensive frozen fish or dump inexpensive rejected longline-caught fish on the local market. The Fisherman's Cooperative has never had widespread support among fishermen, and even members often do not support it by selling their fish elsewhere if offered a higher price. Continued disunity among the troll fishermen hinders them from gaining much political or public support. The charter segment of the fishery remains healthy since only a small portion of revenues are derived from the sale of catches.

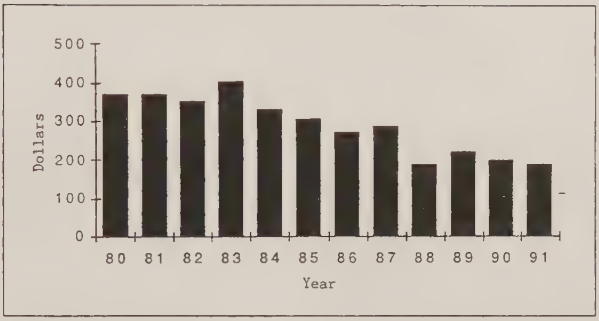

Figure 5.—Inflation adjusted revenue per trolling trip during 1980–91.

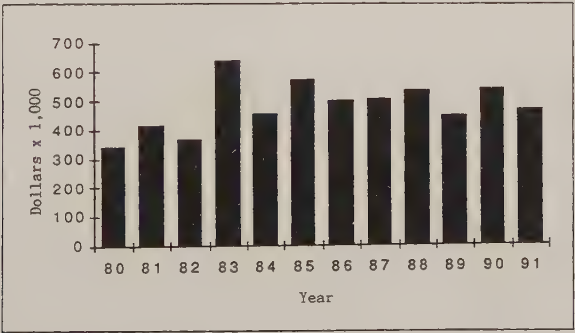

Figure 4.—Inflation adjusted annual revenues for troll-caught pelagic fishes during 1980–91.

## Bottomfish Fishery

Bottomfishing is defined here as fishing from an anchored or drifting boat with hook and line without the aid of floodlights. Guam's bottomfish fishery is a small-scale commercial, subsistence, and recreational fishery that operates primarily from boats <25 feet in length. Nearly all fishing is done by Guam residents from owner-operated vessels, but occasionally tourists and residents fish from relatively large charter boats. Historically, the fishery has experienced considerable fluctuations in annual harvest primarily because of the high turnover rates of a few full-time highliners.

The fishery may be divided into two components based on depth and species. The shallow-water component (<150 m) is the larger of the two and usually targets the red-gilled emperor, *Lethrinus rubrioperculatus*, as well as an assemblage of other emperors, snappers, and groupers. The deep-water component (150–250 m) targets the snapper, *Pristipomoides* spp., complex. A few species (most notably jobfish, *Aprion virescens*, and black jack, *Caranx lugubris*), equally abundant in both the shallow and deep zones, are grouped in the shallow fishery and excluded from the deep fishery for purposes of this paper. The larger size of the shallow-water component is the result of greater participation because of the lower expenditure and relative ease of fishing closer to shore. Small spincasting reels are often used for the shallowest bottomfishing, and electric reels, which may have multiple hooks per line, are used for deeper bottomfishing. Handlines are rarely used. Nearly all participants in the bottomfish fishery also troll for pelagic species, and most participate in both methods on the same trip. All the shallow bottomfish species are coral reef fishes, and they are subject to harvest by both offshore and inshore reef fishery methods. However, only small quantities of the most important bottomfishery species are harvested by these methods, and the most important reef fishery species form a negligible component of the bottomfish fishery.

### *The Catch*

Since 1980 the annual estimated bottomfish catch has fluctuated between 14 and 43 t (Fig. 6). The fluctuations are due primarily to changes in the fishery rather than to changes in the stocks. However, decreasing catches of some of the larger deepwater species are probably stock related. Catches for the past year may be slightly underestimated because of the opening of the Agat Marina which is not yet surveyed. It is believed that a larger proportion of the participation for bottomfish fishing occurs there than at the primary sampling location, the Agana Boat Basin.

Snappers and emperors are the most important bottomfish families, represent an estimated 38.5% and 29.5% of the weight of the harvest from FY1980–91 (Table 1), respectively. Only three other families represented more than 2% of the catch: Groupers (10.0%), jacks (9.4%), and requiem sharks (5.4%). Squirrelfishes, goatfishes, wrasses, dogtooth tuna, and triggerfishes each represented between 1 and 2% of the catch. At least 35 other families collectively represented the remaining 2.6% of the catch. Although sharks collectively represented 5.6% of the catch, they are not targeted and are often killed and discarded at sea. The landed catch is an unreliable indicator of stock size. An estimated 67.7% of the 1980–91 harvest consisted of shallow-water species, and 32.3% consisted of deep-water species.

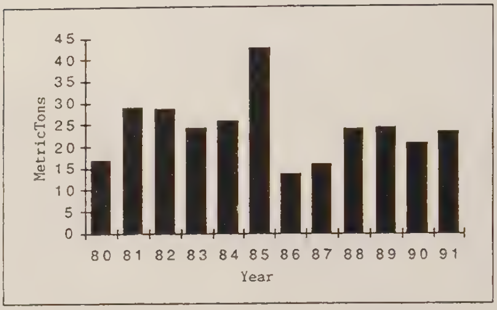

Figure 6.—Estimated annual bottomfish landings during 1980–91.

**Table 1.—Species composition of Guam bottomfish landings during FY 1980–91.**

| | Total landings (kg) | Percent of Total landings | Percent of Shallow portion | Percent of Deep portion |
|---|---|---|---|---|
| Sharks | 14,996.5 | 5.4 | 8.0 | |
| Holocentridae (Squirrelfishes) | 4,259.4 | 1.5 | 2.3 | |
| Serranidae (Groupers) | 27,513.3 | 10.0 | 10.6 | 8.7 |
| *Cephalopholis sonerati* (Tomato grouper) | 3,384.5 | 1.2 | 1.8 | |
| *Epinephelus fasciatus* (Black-tipped grouper) | 9,239.4 | 3.4 | 5.0 | |
| *E. octofasciatus* (Eightbar grouper) | 7,696.7 | 2.8 | | 8.7 |
| *Variola* spp. (Lyretail groupers)[1] | 7,567.9 | 2.8 | 4.1 | |
| Carangidae (Trevallys) | 25,824.7 | 9.4 | 12.2 | 3.5 |
| *Caranx ignobilis* (Giant trevally) | 3,435.5 | 1.2 | 1.8 | |
| *C. lugubris* (Black trevally) | 8,721.4 | 3.2 | 4.7 | |
| *C. melampygus* (Bluefin trevally) | 3,316.2 | 1.2 | 1.8 | |
| *Carangoides orthogrammus* (Yellow-spotted trevally) | 3,685.7 | 1.3 | 2.0 | |
| *Seriola dumerili* (Amberjack) | 3,067.7 | 1.1 | | 3.5 |
| Lutjanidae (Snappers) | 105,844.2 | 38.5 | | |
| Shallow snappers | 26,630.1 | 9.7 | 14.3 | |
| *Aprion virescens* (Jobfish) | 15,294.1 | 5.6 | 8.2 | |
| *Lutjanus bohar* (Red snapper) | 4,174.5 | 1.5 | 2.2 | |
| *L. kasmira* (Bluelined snapper) | 4,099.2 | 1.5 | 2.2 | |
| Deep snappers | 77,716.9 | 28.2 | | 87.5 |
| *Aphareus rutilans* (Lehi) | 10,824.7 | 3.9 | | 12.2 |
| *Etelis carbunculus* (Ehu) | 10,843.1 | 3.9 | | 12.2 |
| *E. coruscans* (Onaga) | 10,511.8 | 3.8 | | 11.8 |
| *Pristipomoides auricilla* (Yellowtail kalekale) | 17,065.5 | 6.2 | | 19.2 |
| *P. filamentosus* (Pink opakapaka) | 6,153.9 | 2.2 | | 6.9 |
| *P. flavipinnis* (Yelloweye opakapaka) | 10,043.7 | 3.6 | | 11.3 |
| *P. zonatus* (Gindae) | 9,712.1 | 3.5 | | 10.9 |
| Lethrinidae (Emperors) | 81,234.6 | 29.5 | 43.6 | |
| *Lethrinus rubrioperculatus* (Redgill emperor) | 66,722.0 | 24.2 | 35.8 | |
| Mullidae (Goatfishes) | 3,880.3 | 1.4 | 2.1 | |
| Sphyraenidae (Barracudas) | 909.3 | 0.3 | 0.5 | |
| Labridae (Wrasses) | 2,981.5 | 1.1 | 1.6 | |
| Acanthuridae (Unicornfishes) | 1,866.9 | 0.7 | 1.0 | |
| Scombridae (Tunas) | 3,208.7 | 1.2 | 1.7 | |
| Balistidae (Triggerfishes) | 3,433.5 | 1.3 | 1.8 | |
| Total nonsnapper deep species | 11,086.0 | 4.0 | | 12.5 |
| Total deep species | 88,785.3 | 32.3 | | 100.0[2] |
| Total shallow species | 186,401.9 | 67.7 | 99.8[2] | |
| Total all bottomfish species | 275,187.2 | 100.0 | | |

[1] Primarily *V. louti* but also includes a small proportion of *V. albimarginata*.
[2] Excludes incidental taxa not tabulated.

The red-gilled emperor is the most important bottomfish species and represented 24.2% of the FY1980–91 estimated harvest, 82.1% of the emperor harvest, and 35.8% of the shallow-water harvest. Other important shallow-water species with percentage of total bottomfish catch indicated, were the jobfish (5.6%); the groupers (*Epinephelus fasciatus*, 3.4%; *Variola louti*, 2.8%; and *Cephalopholis sonerati*, 1.2%); the jacks (*Caranx lugubris*, 3.2%; *Carangoides orthogrammus*, 1.3%; *Caranx melampygus*, 1.2%; and *C. ignobilis*, 1.2%); and the snappers (*Lutjanus bohar*, 1.5%; and *L. kasmira*, 1.5%). The mean sizes of 5 shallow species (*Lethrinus rubrioperculatus*, *Cephalopholis urodeta*, *Epinephelus fasciatus*, *Variola louti*, and *Aprion virescens*) have remained essentially unchanged since 1980 (Davis[2]). The red-gilled emperor, above-listed groupers, and most others in the fishery are small species with high turnover rates. This is indicative of a mature fishery in which the larger species are overfished.

Among the deepwater species, 87.5% consisted of snappers of the *Pristipomoides* complex. The most important species with percentage of total bottomfish catch indicated, were yellowtail kalikali, *Pristipomoides auricilla*, 6.2%; ehu, *Etelis carbunculus*, 3.9%; lehi, *Aphareus rutilans*,

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[2] Davis, G.W. 1992. Territory of Guam 1991 bottomfish fisheries performance. *In* Bottomfish and seamount groundfish fisheries of the western Pacific region. 1991 Annu. Rep. West. Pac. Reg. Fish. Manage. Counc., Honolulu, Hawaii.

3.9%; onaga, *E. coruscans*, 3.8%; yelloweye opakapaka, *P. flavipinnis*, 3.6%; gindai, *P. zonatus*, 3.5%; and opakapaka, *P. filamentosus*, 2.2%. The most important nonsnapper deepwater species were the large eightbar grouper, *Epinephelus octofasciatus*, 2.8%, and the amberjack, *Seriola dumerili*, 1.1%. Grouper was rarely caught and did not even appear in the sampled catch during most years. Also, catches of onaga, another large and the most highly prized of the deepwater snappers, decreased considerably during the past 6 years. Sample sizes for both of these species were inadequate for year-to-year comparisons, and in some years they were not even encountered in the survey. However, the mean sizes of five important species (*Pristipomoides auricilla, P. flavipinnis, P. zonatus, Etelis carbunculus*, and *Aphareus rutilans*) have remained essentially unchanged since 1980 (Davis[2]).

### *Participation and Effort*

The estimated number of vessels in the bottomfish fishery has increased significantly over the past 12 years from 24 to 173 boats in 1991 ($r^2$ = 0.702, P<0.001). The current number could be higher since the Agat Marina, which opened in early 1991, is not sampled. However, long-term trends in overall effort as boat trips and boat hours are not apparent (Fig. 7). This apparent contradiction is due to the effects of a few commercial highliners that dropped out of the fishery in 1986. There has been a short-term trend toward increasing effort since then, and this is expected to continue.

### *Catch Rates*

The annual catch rate for the bottomfish fishery has decreased significantly over the past 12 years (Fig. 8; $r^2$ = 0.718, P<0.001). This may be a result of a few commercial highliners dropping out of the fishery after 1985. With the exception of 1983, catch rates were significantly higher (3.4–3.6 kg/boat-hour) for 1980–85 than all years since then (2.3–2.8 kg/boat-hour). However, the catch rate has remained steady since 1986, indicating that the fishery is stable.

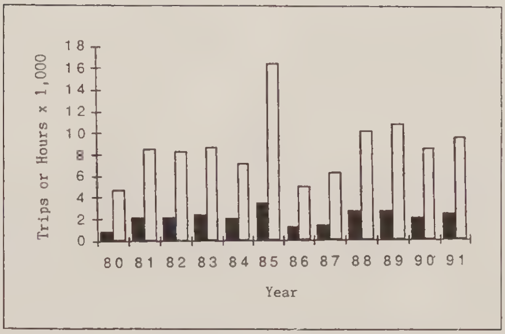

Figure 7.—Estimated annual number of boat trips and boat hours for the bottomfish fishery during 1980–91.

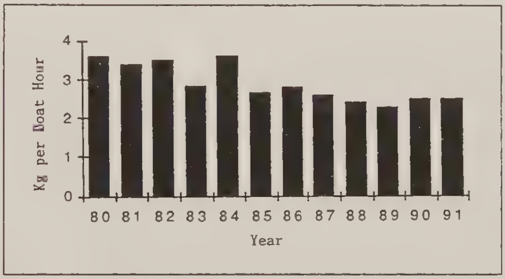

Figure 8.—Catch rates (kg/boat-hour) for the bottomfish fishery during 1980–91

### *Economics*

Nearly all of Guam's bottomfish fishermen hold jobs outside the fishery, and only a small minority sell their catch. However, high turnover rates among a few full-time highliners have greatly influenced annual catch and effort estimates, particularly prior to 1986. Over the past 12 years, an estimated 31% of the bottomfish catch entered the commercial market with annual inflation-adjusted revenues ranging from $22,994 to $114,176 (Davis[2]; Fig. 9). After a 1983 peak, revenue per trip declined sharply and has remained between $103 and $159. Inflation-adjusted average price of bottomfish has remained between $5.64 and $7.67 /kg during the past 12 years. The trend has been a slow and steady decline offset by a sharp rise between 1988 and 1989. Although the supply for fresh local bottomfish has never met the demand, competition from inexpensive imports from the neighboring islands has kept the price depressed and is expected to continue to do so.

## Reef-fish Fishery

Guam's reef-fish fishery is composed of several fisheries based on method and logistics. The bulk of the fishery is shore-based (Hensley and Sherwood, 1993) and not considered here. The boat-based portion consists primarily of spearfishing and, to a minor extent, of other methods also used in the shore-based fishery. The minor methods include the use of various nets, spin-casting, and gleaning. Since these methods are infrequently encountered, not expanded separately, and collectively represent less than 1% of the annual estimated boat-based harvest, they are not considered here.

Nearly all spearfishing activity with boats occurs from owner-operated

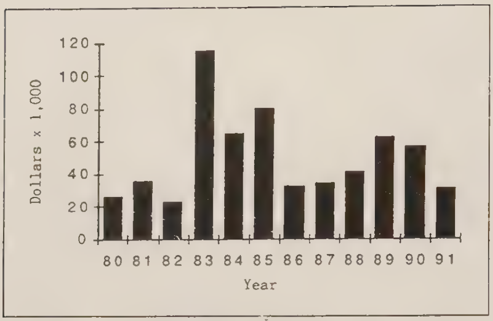

Figure 9.—Inflation adjusted annual revenues for the bottomfish fishery during 1980–91.

rather than chartered boats. The fishery is highly seasonal and the highest mean monthly participation, effort, and landings occur in June, the lowest in March. This seasonality is due to weather and sea conditions which render northwestern clockwise through southeastern exposures inaccessible because of high seas and surf. The fishery consists of two components based on whether or not scuba equipment is used. The range of species targeted is quite broad and includes nearly all coral reef-dwelling finfishes ≥12 cm, crustaceans, and mollusks, the latter picked up by hand incidentally. There is considerable overlap among species targeted by the shore-based spearfishing fishery and shallow bottomfish fishery. Estimates of participation, effort, and catch are crude since it is difficult to get statistically useful sample sizes. Spearfishing is an infrequently encountered method that often occurs outside the surveyed time-frame, and tends to occur more frequently from under- or unsampled launch sites. Considerable spearfishing activity occurs at night and parties return between 2100 and 2400 hours. Since this component of the fishery was not monitored until FY 1985, only information beginning with that year is considered here. Estimates of catch and effort are given for calendar years, but species composition is available only for fiscal years.

### The Catch

Annual catch estimates since 1985 have varied widely from 5 to 17 t with a trend toward increased landings (Fig. 10). Prior to 1989 the bulk of the catch was caught by snorkelers, but for the past 3 years 50% or more of the landings have been caught by scuba divers. A broad range of species is targeted including nearly all coral reef dwelling finfishes ≥12 cm as well as incidental crustaceans and mollusks. Over 100 species have been observed in a given survey year, and probably another 50 species are landed but not encountered by the survey.

Since FY1985, 36% of the catch has consisted of parrotfishes (Scaridae), followed by surgeonfishes (Acanthuridae, 19%), and wrasses (Labridae, 7%) (Table 2). Other important finfish families include the groupers (6%), rudderfishes (5%), snappers (3%), jacks (3%), and squirrelfishes (2%). The most important invertebrates are spiny lobsters (4%), primarily *Panulirus penicillatus* which are speared, and topshell (2%) which are picked up by hand. Higher proportions of wrasses, groupers, rabbitfishes, parrotfishes, goatfishes, sweetlips, and spiny lobsters are caught by scuba divers than by snorkelers (Table 2). Greater differences occur at the species level since many species typically inhabit depths beyond the reach of most snorkelers. There are also distinct differences between day and night catches, but separate day and night expansions have not been run.

### Participation and Effort

The estimated annual number of boat trips and person trips has fluctuated widely since 1985, ranging from 279 to 1,057 and from 748 to 3,330, respectively. The estimated annual number of boat hours and person hours has also fluctuated widely, ranging from 894 to 2,151 and from 2,293 to 7,119, respectively (Fig. 11).

### Catch Rates

Overall catch rates as kg/boat-hour and kg/person-hour have ranged from 5.2 to 9.4 and from 1.5 to 3.1 since 1985, respectively (Fig. 12). The catch rate for the scuba segment has risen sharply over the last 2 years. This is not believed to be indicative of a healthy fishery for nonbiological reasons that are not apparent from the

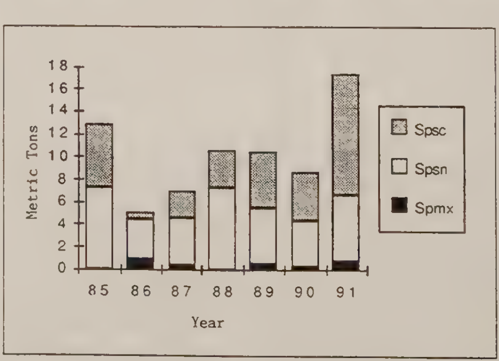

Figure 10.—Estimated annual spearfishing landings utilizing small boats during 1985–91. Spsc = landings exclusively by scuba diving; Spsn = landings exclusively by snorkeling; Spmx = landings by a combination of scuba diving and snorkeling.

Table 2.—Species composition of Guam landings taken by divers during FY 1985–91. All fishes were taken by spear, and invertebrates were taken by hand as well as spear. Taxa comprising less than 1% of total landings are not shown.

| | Snorkel only | | Scuba only | | Unknown or both | | All methods | |
|---|---|---|---|---|---|---|---|---|
| Taxon | kg | % | kg | % | kg | % | kg | % |
| Fishes | | | | | | | | |
| Carcharhinidae | | | | | | | | |
| (Requiem sharks) | 502.3 | 1.4 | 189.2 | 0.6 | 0.0 | 0.0 | 691.5 | 1.0 |
| Holocentridae | | | | | | | | |
| (Squirrelfishes) | 744.2 | 2.1 | 585.7 | 1.8 | 89.5 | 3.4 | 1,419.4 | 2.0 |
| Serranidae (Groupers) | 1,390.1 | 3.8 | 2,714.0 | 8.4 | 78.2 | 2.9 | 4,182.3 | 5.9 |
| Carangidae (Jacks) | 1,545.0 | 4.3 | 210.8 | 0.7 | 25.5 | 1.0 | 1,781.3 | 2.5 |
| Lutjanidae (Snappers) | 910.8 | 2.5 | 978.9 | 3.0 | 58.6 | 2.2 | 1,948.3 | 2.7 |
| Haemulidae (Sweetlips) | 314.1 | 0.9 | 909.2 | 2.8 | 18.5 | 0.7 | 141.8 | 1.7 |
| Lethrinidae (Emperors) | 643.3 | 1.8 | 435.8 | 1.3 | 58.1 | 2.2 | 1,137.2 | 1.6 |
| Mullidae (Goatfishes) | 408.3 | 1.1 | 518.7 | 1.6 | 56.5 | 2.1 | 983.5 | 1.4 |
| Kyphosidae (Rudderfishes) | 3,241.1 | 8.9 | 311.3 | 1.0 | 48.9 | 1.8 | 3,601.2 | 5.1 |
| Mugilidae (Mullets) | 755.7 | 2.1 | 0.0 | 0.0 | 0.0 | 0.0 | 755.7 | 1.1 |
| Labridae (Wrasses) | 1,524.1 | 4.2 | 3,175.6 | 9.8 | 477.1 | 17.9 | 5,176.8 | 7.3 |
| Scaridae (Parrotfishes) | 12,238.9 | 33.7 | 13,152.9 | 40.7 | 394.5 | 14.8 | 25,786.3 | 36.2 |
| Acanthuridae | | | | | | | | |
| (Surgeonfishes) | 7,215.8 | 19.9 | 5,987.2 | 18.5 | 341.3 | 12.8 | 13,544.3 | 19.0 |
| Other fishes | 868.4 | 2.4 | 923.4 | 2.9 | 79.1 | 3.0 | 1,870.7 | 2.6 |
| Total | 32,301.9 | 89.0 | 30,092.7 | 93.1 | 1,725.8 | 64.9 | 64,120.1 | 90.0 |
| Invertebrates | | | | | | | | |
| *Trochus niloticus* (Topshell) | 807.7 | 2.2 | 197.9 | 0.6 | 604.7 | 22.7 | 1,610.3 | 2.3 |
| *Tridacna maxima* | | | | | | | | |
| (Giant clam) | 1,194.1 | 3.3 | 6.7 | 0.0 | 0.0 | 0.0 | 1,200.8 | 1.7 |
| *Octopus* spp. (Octopus) | 441.9 | 1.2 | 208.6 | 0.6 | 104.8 | 3.9 | 755.3 | 1.1 |
| *Panulirus* spp. | | | | | | | | |
| (Spiny lobsters) | 1,214.0 | 3.3 | 1,635.5 | 5.1 | 130.8 | 4.9 | 2,980.3 | 4.2 |
| Other invertebrates | 326.4 | 0.9 | 194.6 | 0.6 | 92.9 | 3.5 | 613.9 | 0.9 |
| Total invertebrates | 3,984.1 | 11.0 | 2,243.3 | 6.9 | 933.2 | 35.1 | 7,160.6 | 10.0 |
| Method totals | 36,286.0 | 100.0 | 32,366.0 | 100.0 | 2,659.0 | 100.0 | 71,280.4 | 100.0 |
| Percent of total catch | | 50.9 | | 45.4 | | 3.7 | | 100.0 |

summary statistics. These include greater success at intercepting scuba diving spearfishing parties, particularly those returning late at night, and a shift in effort to deeper water (30–42 m) by parties that consider shallow areas "fished out."

### *Economics*

Spearfishermen often sell their catch, but no economic information is available. Catch disposition is recorded but has never been analyzed. Competition from inexpensive imports probably inhibits growth, which slows the potential for overfishing.

## Bigeye Scad Fishery

The bigeye scad, locally called atulai, is a small coastal pelagic species that is cosmopolitan in the tropics, but probably forms a distinct stock in the Marianas. It periodically occurs in large schools in coastal bays and channels as well as from near the surface to depths of >200 m near shore. It typically aggregates inshore during the day and migrates offshore at night. When inshore, bigeye scad are taken by a variety of shore-based methods including teams of people using large barrier nets with the aid of boats and divers. When offshore, they are attracted to lights hung from small boats and jigged. Shore-based methods typically account for 70% or more of the annual landings (Hensley and Sherwood, 1993).

Jigging for bigeye scad by nightlight is done during moonless periods. Prior to 1985, too few returning fishermen were intercepted by the survey, so only the period 1985 through 1991 is presented here. The fishery is highly seasonal; the greatest effort and catches occured during July and August and there is almost no activity or catches from December through April.

### *The Catch*

Estimated annual landings since 1985 have ranged from 3.4–20.2 t with no apparent trend. Good and poor years coincide well with estimated annual landings by shore-based methods (Hensley and Sherwood, 1993), indicating that these results are real rather than the result of inadequate sample size. The largest estimated combined annual catch for Guam for all methods was 76.5 t in 1989. An upper bound of 200 to 440 t for an annual range of harvest for the entire Mariana Archipelago has been suggested (Polovina et al., 1985). This is based on the untested assumption that the abundance per mile of 200 m contour in the Marianas is the same as that in the Hawaiian Islands. For Guam and Galvez-Santa Rosa Banks, the equivalent upper yield would be 50–112 t. No figure is available for Rota Banks and 45° Banks.

### *Participation and Effort*

The estimated annual number of boat trips and person trips has fluctuated

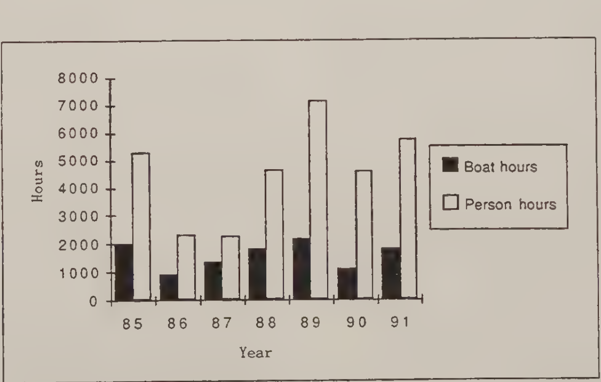

Figure 11.—Estimated annual number of boat hours and person hours spent spearfishing during 1985–91.

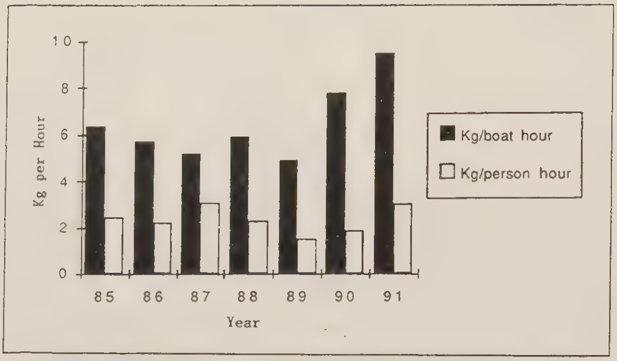

Figure 12.—Catch rates as kg per boat hour and kg per person per hour spent spear-fishing during FY 1985–91.

widely since 1985, ranging from 325 to 1,280 and from 911 to 3,475, respectively. The estimated annual number of boat hours and person hours has also fluctuated widely, ranging from 2,167 to 9,385 and from 5,312 to 26,088, respectively. No clear trends are apparent.

### *Catch Rates*

Catch rates since 1985 have ranged from 1.0 to 3.8 kg/boat-hour and from 0.4 to 1.4 kg/person-hour, respectively, with no apparent trend or correlation with annual landings.

### *Economics*

Bigeye scad are sold by subsistence and commercial fishermen along the roadside, in stores, or directly to restaurants. Bigeye scad and closely related species are also imported fresh from the Philippines. Neither the proportion of the annual harvest that is sold nor revenues have been estimated for this fishery although some sales information is available on the offshore survey data base. An assessment of the economics of this fishery is not possible at this time. Since bigeye scad are usually the single most important inshore species in terms of annual landings, their economic importance must be great.

## Discussion

### Pelagic Fishery

At present, trolling is the only method used by Guam's small-boat fishery that targets pelagic species. The targeted species are all migratory, high-trophic-level predators. Fish caught in the vicinity of Guam are part of regional or possibly Pacific-wide stocks. Although some species may linger in the vicinity of Guam for a while, they are generally seasonal in occurrence, have very high fecundity, and grow fast. Pelagic species that spend at least the daylight hours >50 m (broadbill swordfish, *Xiphias gladius*; bigeye tuna, *Thunnus obesus*; and albacore, *Thunnus alalunga*) are not locally fished, although there is commercial interest in them.

Annual landings of Guam's troll-caught species are highly variable. There are no apparent trends in the catches of mahimahi, wahoo, skipjack tuna, or sailfish. Catches of blue marlin increased during the past 12 years, whereas catches of yellowfin tuna decreased. Catch rates for blue marlin have increased in recent years, whereas catch rates for skipjack and yellowfin tuna have declined. Increasing charter boat participation and interest in sportfishing rather than commercial fishing are likely causes of increasing catches and catch rates for blue marlin. The low marketability of skipjack tuna is the most likely cause for declining catch rates for that species, but declining catches and catch rates for yellowfin tuna may be stock related. These two tunas as well as bigeye tuna are the principal components of the Guam-based domestic purse seine and foreign longline fisheries which operate primarily in more southern Federated States of Micronesia waters. The impact of these large-scale fisheries on stocks of these, as well as incidentally caught mahimahi, wahoo, blue marlin, and sailfish, are largely unknown, and the data necessary to assess this are not available to U.S. fisheries scientists. However, landings of longline-caught tuna transshipped through Guam are being collected by the Guam Department of Commerce; the South Pacific Commission is collecting data on the purse seine fishery and has a major tagging study of yellowfin tuna in progress. The most complete assessment of blue marlin to date (Skillman, 1989) indicates that it is growth overfished, but that the situation may be improving because of increased use of deep vs. shallow longline gear.

A major complaint by troll fishermen is that they must now travel farther to obtain the same catches they once enjoyed closer to Guam. To evaluate this apparent indicator of possible overfishing, a detailed analysis of catch rates by primary fishing area must be done. Although the necessary information is on the data base, outmoded computer equipment and a shortage of personnel have prevented such an analysis. With the possible exception of yellowfin tuna, there is no other indication of overfishing.

Management of the local pelagic fishery is meaningless because Guam's small trolling fleet does not have the potential to affect the stocks. However, certain beneficial measures have and could be taken. The deployment of FAD's probably helps to attract and hold migrating pelagics closer to Guam. The banning of longlining within 50 miles of the 100-fm contour of Guam and its satellite banks reduces the risk of gear conflicts and prevents the interception of pelagics once they are within the range of the trolling fleet. A similar ban on domestic purse seiners could also benefit the troll fishery, but this is highly unlikely on legal grounds.

The charter and recreational components of the fishery are economically healthy, and continued growth is expected. However, the health of the commercial component is in decline because of a combination of competition from cheaper, more efficient sources including longline-caught fishes rejected for transshipment and the absence of a unified local marketing effort.

### Bottomfish Fishery

The bottomfish fishery appears to be stable, but the dominance of small species with high turnover rates is indicative of a mature fishery in which the larger, long-lived species are overfished. Indeed, two of the most important, desirable, and largest of the deep-water species in "virgin" catches have nearly disappeared in recent years. The grouper *Epinephelus octofasciatus*, which represented 13% of the catch (90% of which were the deep-water component) in the late 1960's and was a prominent component of catches in the relatively unexploited Commonwealth of the Northern Mariana Islands in the early 1980's (Ikehara et al., 1970; Polovina et al., 1985), is now rarely caught and has not even appeared in the sampled catch for most years since 1980. Catches of onaga, *Etelis coruscans*, the single most important species in catches of the late 1960's (25%), have decreased considerably during the past 6 years. However, unchanging mean sizes of 10 important bottomfish species since 1980 (5 shallow and 5 deep) indicate that the fishery is stable.

Polovina and Ralston (1986) calculated an annual equilibrium yield for the 125–275 m depth band of 15.6 t for Guam and 7.8 t for the Galvez-Santa Rosa Banks region (23.4 t total, but this excludes the smaller Rota and 45° banks). The mean annual harvest for the 1980–91 period was about 24 t, 7 of which were deepwater species. The largest estimated annual deepwater harvest was 12.8 t (42.8 t in 1985 for all depths), well under the estimated equilibrium yield. For the fishery as a whole, there is no indication of overfishing.

Since it is impossible to target a given species reliably and the viability of released deep-water species is unlikely, species-specific management measures would not be practical. At some point, a value judgement must be made whether or not to sacrifice the most vulnerable species in return for increased overall yields. Assuming that there is a single archipelagic stock, then as long as there are refuges in the form of lightly fished banks or islands sufficient to insure an adequate spawning stock biomass of key species, no specific management measures are necessary.

The economics of the fishery is complex and poorly understood. Although supply has never met the demand, several factors probably limit participation. These include competiton from inexpensive imports of reef and bottomfishes and a booming economy that offers better opportunities elsewhere. No one depends on bottomfishing to earn a living. There have been no full-time commercial highliners since the mid-1980's, and increasing annual landings since then are attributable to an increase in the number of participants which are probably primarily recreational and subsistence fishermen.

More effective management of the fishery would be facilitated by a clear separation of deep- and shallow-water effort as well as catches and better consideration of the overlap and interaction of the shallow water component with other competing fisheries. Biological studies of key species are desirable.

### Reef-Fish Fishery

Spearfishing is the only significant reef-fish fishery other than the shallow bottomfish fishery which uses small boats. The same stocks are also harvested by shore-based spearfishing as well as other methods. Catch rates have increased during the past 3 years primarily because of an increase in the use of scuba equipment and the tendency of certain "highliners" to shift to deeper water. The sample size is insufficient for statistically significant trends to be detected. To date, biological data on the species have not been examined, nor have there been any studies of the biology of key species. However, anecdotal information suggests that some species, if not the fishery as a whole, are overfished. There is universal agreement among long-time spearfishermen that catches are down considerably from several years ago, and that one has to travel to the least accessible areas or to visit deeper water to obtain worthwhile catches. This author as well as other divers have noticed a decline in many of the larger species during the past 15 years. In comparison to other relatively unfished islands in the region, the community structure of Guam's reef fishes was noticeably different as long as 15 years ago and dominated not only by small species that mature rapidly but also by relatively small individuals of many species. There also seems to be a trend among divers in general, particularly the transient military and nonindigenous population, to take up nonconsumptive activities such as photography. Since this group consists primarily of those with relatively low spearfishing skills, the remaining skilled fishermen could cause the catch rate to increase until biological reasons impact it. However, no statistical significance can be attached to apparently increasing catch rates in recent years because of high variability and small sample sizes.

De facto refugia in the form of seasonal rough water as well as less accessible islands in the CNMI and offshore banks may prevent recruitment overfishing for many species. However, many lagoon and reef-flat species do not benefit from this and are under considerable fishing pressure at Rota and Saipan, the only other islands with these habitats.

New management measures are needed to prevent a decline in this fishery. A network of permanent preserves that encompass a diversity of habitats and that are large enough to ensure the protection of the more mobile and larger, more vulnerable species is needed. This would also reduce the potential for conflicts by satisfying the demands of nonconsumptive users. Species-specific management of the most vulnerable species is also desirable. Restriction of certain practices such as the commercial sale of speared fish or the use of scuba to spear fish, particularly at night, should be considered.

Although no economic information has been summarized, the supply has never met the demand. However, competition from inexpensive imports keeps prices low and may reduce the pressure on the resource.

### Bigeye Scad Fishery

Estimated annual landings since 1985 have fluctuated widely. Good and poor years coincide well with estimated annual landings by shore-based methods, indicating that these results are real rather than the result of inadequate sample size. There is no indication of overfishing. Since the largest estimated combined annual catch for Guam for all methods—84.3 t—falls midway between suggested upper equilibrium yields based on studies in the Hawaiian Islands, this fishery should be closely monitored.

## Acknowledgments

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# A Review of Interactions Between Hawaii's Fisheries and Protected Species

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*ABSTRACT—Several fisheries in Hawaii are known to have interactions with protected cetaceans, seabirds, marine turtles, or seals. Handline fisheries for bottomfish, tuna, and mackerel scad lose bait and catch to bottlenose dolphins, rough-toothed dolphins, and Hawaiian monk seals. Troll fisheries for billfish lose live bait to bottlenose dolphins, rough-toothed dolphins, albatrosses, and boobies; these fisheries may also lose catch to false killer whales. A longline fishery for tuna and billfish has burgeoned in Hawaii since 1987, resulting in interactions with protected species; marine turtles, seabirds, and monk seals take bait and are known to become hooked, and false killer whales may take catch. Research on deterrents or alternative fishing methods has been limited, and interactions have been reduced primarily through management and regulatory actions. These include area closures and gear requirements. An observer program has also been established for the bottomfish and longline fisheries.*

## Introduction

Interactions involving commercial fisheries and small odontocetes protected by Federal statutes have occurred in Hawaii since 1948 (Schlais, 1984, 1985), and reports from fishermen about small cetaceans stealing catch and bait continue to surface periodically throughout the Hawaiian Islands. Several species of sea turtles and whales are also involved in fisheries through entanglement or accidental hooking. The threatened and endangered species involved in fishery interactions are the Hawaiian monk seal, *Monachus schauinslandi*; humpback whale, *Megaptera novaeangliae*; leatherback turtle, *Dermochelys coriacea*; olive ridley turtle, *Lepidochelys olivacea*; loggerhead turtle, *Caretta caretta*; hawksbill turtle, *Eretmochelys imbricata*; and green sea turtle, *Chelonia mydas*. Nonendangered marine mammals identified as interacting with commercial fisheries in Hawaiian waters include bottlenose dolphins, *Tursiops truncatus*; false killer whales, *Pseudorca crassidens*; rough-toothed dolphins, *Steno bredanensis*; and spinner dolphins, *Stenella longirostris*. Among seabirds, which are protected by the Migratory Bird Treaty Act of 1918, albatrosses, *Diomedea* sp.; and boobies, *Sula* sp., are reported involved in fishery interactions.

This paper describes protected species interactions with Hawaiian commercial fisheries on a fishery by fishery basis. Hawaiian commercial fisheries will include the areas fished by the distant water fleets originating from Hawaii even if outside of the 200-mile Exclusive Economic Zone (EEZ) surrounding the Hawaiian Archipelago. Efforts to document and resolve protected species/fishery interactions will also be described.

## Biology and Status of Protected Species

### Small Cetaceans

Four species of small cetaceans interact with fisheries in Hawaii, but three (bottlenose dolphin, rough-toothed dolphin, and false killer whale) occur pelagically as well as within the Archipelago. Animals which are sighted inshore and interact with fisheries may mix with their pelagic conspecifics, but the extent of such movement is not known.

The bottlenose dolphin is found throughout the Hawaiian Archipelago, usually within five miles of emergent land or shallow banks (Shallenberger, 1981). School sizes range from single or small groups of 3–10 animals to aggregations of more than 100 (Tomich, 1986). A combined aerial and vessel survey of inshore waters adjacent to Oahu, Molokai, Lanai, Maui, and Hawaii documented a minimum of 430 individuals[1].

The rough-toothed dolphin is found near all major islands within the Archipelago (Tomich, 1986), and at least as far north as French Frigate Shoals (JRH, personal observ.). No estimates of abundance exist. At least 23 were collected from Hawaiian waters for oceanaria in 1963–81 (Shallenberger, 1981).

The false killer whale is found near all the main islands, but its occurrence and distribution in the Northwestern Hawaiian Islands (NWHI) is unknown. An aerial survey of the lee areas of Oahu, Lanai, and Hawaii documented a minimum of 470 individuals, all of which were sighted along the northwestern coast of Hawaii[2].

Spinner dolphins occur in relatively discrete schools frequenting inshore bays and lagoons within the Archipelago, from the island of Hawaii to Kure Atoll. The largest school (200 – 250 animals) occurs along the west coast of Hawaii from Honokohau Harbor to Kiholo Bay (Norris and Dohl, 1980). Schools disperse to deep water at night to feed and return inshore to rest during the day. Some mixing of animals between schools may occur during feeding forays.

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[1] Naval Ocean Systems Center, Kaneohe Marine Corps Air Station, Kaneohe, HI. 1987. Unpubl. aerial survey data.

[2] S. Leatherwood and R. R. Reeves. Aerial survey for false killer whales off Hawaii, June 1989. 2146 Fort Stockton Dr., San Diego, CA 92103. Unpubl. rep., 13 p.

### Humpback Whale

Humpback whales that winter in Hawaii are part of the North Pacific population, estimated at 1,200 – 2,000 animals (Johnson and Wolman, 1984; Darling and Morowitz, 1986; Baker and Herman, 1987). The Hawaiian stock is estimated at 1,407 ± 294 (95% confidence limits) whales (Baker and Herman, 1987). These whales begin arriving from North Pacific summer feeding grounds in December. The number of whales peaks in late January through February. In April, they begin migrating out of Hawaiian waters, and by late May or early June the last whales usually have departed. A few animals have been sighted in the NWHI[3].

### Hawaiian Monk Seal

The only seal native to the Hawaiian Islands, the Hawaiian monk seal, is found around all of the NWHI and is occasionally seen in the main islands. The major pupping islands are in the NWHI. The total population for the five major breeding locations plus Necker Island in 1987 was estimated to be 1,718 seals[4] including 202 pups of the year (Gilmartin[5]). Significant declines in pupping and juvenile survival, particularly at French Frigate Shoals since 1989, are cause for concern for this endangered species.

### Sea Turtles

Five species of sea turtle interact with fisheries in Hawaii, but only one, the green sea turtle, nests in large numbers in the Archipelago and represents a distinct population. There are isolated nesting sites for hawksbill turtles in the main Hawaiian Islands, primarily on the islands of Hawaii and Molokai. The remaining three species nest elsewhere in the Pacific Basin.

Leatherback turtles are commonly seen by fishermen in Hawaiian offshore waters, generally beyond the 100 –fathom contour but within sight of land. Sightings often occur off the north coast of Oahu and the west coast of Hawaii. The pelagic zone surrounding the Hawaiian Islands likely constitutes foraging habitat and migratory pathways for this species. A high-seas aggregation of leatherbacks is known to occur north of the Hawaiian Islands at lat. 35°– 45°N, long. 175°– 180°W (Balazs et al.[6]; Skillman and Balazs, 1992). The nesting habitat and origin of these turtles are not known.

Available information suggests that the olive ridley turtle regularly uses the Hawaiian pelagic region for foraging and/or developmental migrations. Olive ridleys in reasonably good health have been found entangled in scraps of net or other floating synthetic debris. Small crabs, barnacles, and other marine life often reside on the debris and likely serve as food attractant to turtles. Juvenile and subadult olive ridleys are among the life stages known to be present in Hawaiian waters. Olive ridleys found in Hawaiian waters are probably derived from the eastern Pacific breeding aggregation of Mexico (Balazs et al.[6]).

The loggerhead turtle is a cosmopolitan species found in temperate and subtropical waters. Nearly all nesting occurs north of 25°N or south of 25° S. Adult loggerheads undertake long reproductive migrations between their nesting sites and foraging areas. However, their dispersal patterns in foraging areas are not well known for any population. In the North Pacific the only major nesting beaches are in the southern part of Japan (Dodd, 1988). Although reliable counts are not available, as many as 2,000 –3,000 loggerheads may nest annually on beaches throughout Japan. Immature loggerheads encountered during driftnet fishing in the North Pacific may originate from nesting beaches in Japan, being transported to the north and east by the Kuroshio Current and its extension (Wetherall et al., In press). Loggerheads reported taken in the Hawaiian longline broadbill swordfish fishery may be of the same origin.

The green sea turtle is found throughout the Hawaiian Archipelago. Its distribution, however, has been reduced in recent historical times; breeding aggregations have been eliminated, and certain foraging areas are no longer used in the main Hawaiian Islands (Balazs, 1980; Balazs, et al., 1987). More than 90 percent of the breeding and nesting activity of Hawaiian green turtles occurs at French Frigate Shoals, in the NWHI. The number of females nesting there fluctuates annually. An annual mean as high as 300 was recorded during 1973–1982. The total mature female population at French Frigate Shoals is estimated to be approximately 750 animals (Balazs et al.[6]).

### Seabirds

All five species of seabirds known to interact with fisheries nest on remote islands throughout the Archipelago. Recent estimates of abundance in Hawaii are 683,500 breeding pairs for the two albatross species[7], and 6,590–7,950 breeding pairs for the three species of booby (Harrison et al., 1984).

## Fishery Interactions

Interactions between cetaceans and fisheries have been documented in Hawaii since at least the late 1940's and were exacerbated by installation in 1979 of a deep-water buoy as part of the Ocean Thermal Energy Conversion (OTEC) project west of the island of Hawaii (Schlais, 1984, 1985). This buoy proved very productive as a fish aggregating device, was popular with fisherman from Kona, and became well known for schools of dolphins stealing bait and catch. Interactions further increased in the early 1980's with the deployment of fish aggregation devices (FAD's) by the Hawaii Division of Aquatic Resources throughout state waters. Specific fisheries and the species involved have been documented by Mate (1980), Shallenberger (1981), and Kuljis[8].

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[3] M. Craig, Southwest Fisheries Science Center, Honolulu Laboratory, 2570 Dole St., Honolulu, HI 96822–2396. Personal commun. 1993.

[4] This estimate utilizes counts of adult males at Lisianski made during the late summer molting season, which confounds the total estimate somewhat because beach counts at the other islands were conducted in the spring.

[5] W. G. Gilmartin. 1988. The Hawaiian monk seal: Population status and current research activities. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab.,. Southwest Fish. Cent. Admin. Rep. H-88-17, 14 p.

[6] G. H. Balazs, H. F. Hirth, P. Y. Kawamoto, E. T. Nitta, L. H. Ogren, R. C. Wass, and J. A. Wetherall. 1992. Interim recovery plan for Hawaiian sea turtles. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Honolulu Lab., Southwest Fish. Sci. Cent. Admin. Rep. H-92-01, 76 p.

[7] E. Flint, U.S. Fish and Wildlife Service, Pacific/Remote Islands NWR Complex, P.O. Box 50167, Honolulu, HI 96850. Personal commun. 1993.

Interactions may be divided into two basic types in this region. One involves the loss of catch or bait with little or no impact to the individual animals from the fishing gear or technique, short of aversive action taken by the fishermen. The other is the hooking or entanglement of animals in gear whether or not catch or bait is the primary stimulus for interactions. While documenting these two types of interactions is relatively straightforward, investigating how these take place, assessing the impact on fisheries and protected species, and developing solutions to incidental take and loss of catch are much more difficult.

Loss of catch is documented through observer reports, interviews with fishermen, and reports directly from fishermen through fish catch/interaction logs. Entanglements and hookings are reported in the same manner.

### Handline Fishery for Bottomfish

Boats in this fishery use 3–6 lines, each with 6–15 hooks, usually baited with squid. Hooks are spaced in approximately 0.5 m intervals and are fished at depths of 120–250 m. A chum bag containing chopped fish or squid may be suspended above the highest of these hooks. The gear is pulled after several fish are hooked. Locations for this fishery include the main islands as well as banks in the NWHI.

Both bait and catch have been reported lost to bottlenose dolphins, and schools of dolphins have been reported following fishing boats, particularly in the NWHI. Danger to fishermen results when a dolphin jerks a fish from a hook; the dolphin may pull 10–15 m of line from the fisherman's hands, exposing the fisherman to the risk of open hooks. Interactions with dolphins have been reported off the island of Hawaii, Kaula Island, and several banks in the NWHI. Dolphins may be attracted by undersized fish or unmarketable species (e.g., kahala, *Seriola dumerili*) which are discarded during fishing operations. In some cases after consuming a few fish the dolphins will continue to remove fish from the lines and "play" with them.

Interactions between Hawaiian monk seals and the bottomfish fishery have occurred in the main Hawaiian Islands and the NWHI. A female Hawaiian monk seal was observed with an "ulua" hook in its mouth on Kauai in October 1989. The hook was removed from the seal with no apparent serious aftereffects[9]. A Hawaiian monk seal was photographed at French Frigate Shoals with a bottomfish hook in its mouth in 1982. The seal was later observed alive without the hook (Henderson, 1985). Like dolphins, monk seals may be attracted by discarded bycatch (Fig. 1).

Reports of monk seals and bottlenose dolphins taking bottomfish off fishing lines from around Necker Island and Kaula Island were received from commercial fishermen in 1983–1987[10]. In 1991 and 1992 observer trip reports from the bottomfish fishery documented monk seals and bottlenose dolphins taking fish off of lines in the NWHI. A rate of one interaction event/34.4 hours of fishing was calculated for monk seals and a rate of one interaction event/24.3 hours for bottlenose dolphins based on observer reports through July 1992[11].

### Day Handline Fishery (Palu-ahi) for Tuna

Boats in this fishery use 3–5 lines, each with a single hook, baited with mackerel, mackerel scad, or squid, and fished at a depth of up to 150 m. The fishery targets both skipjack and yellowfin tuna. The location for this fishery is primarily off the southeast and west coasts of the island of Hawaii, often in association with FAD's in other areas of the main Hawaiian Islands as well. Bottlenose dolphin and rough-toothed dolphin take both bait and catch.

### Night Handline Fishery (Ika-shibi) for Tuna

Bigeye tuna and yellowfin tuna are taken in this night handline fishery at the edge of the island shelf near the 1,000 fathom contour from 2 to 20 km from shore. This fishery occurs predominantly south of the island of Hawaii from Hilo to around Captain Cook, but also occurs around FAD's throughout the main islands. The boats use 20 –30 watt bulbs underwater or over the surface to attract squid, *Stenoteuthis oualeniensis* which is caught for bait or market. Other baits include frozen mackerel or squid. The bait is typically fished at 30 m depth. Loss of catch and bait as well as poor catch rates have been attributed to bottlenose dolphins. Poor catch has also been attributed to sharks.

### Handline Fishery for Mackerel Scad

This fishery takes place at night, primarily off the west shores of Oahu and the island of Hawaii. Lights are used to illuminate an area around the boat, and a line with several hooks, either

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[8] B.A. Kuljis. 1983. Porpoise/fisheries interactions within the Hawaiian Islands. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-88-19C, 16 p.

[9] W. Gilmartin. Southwest Fisheries Science Center, Honolulu Laboratory, 2570 Dole St., Honolulu, HI 96822-2396. Personal commun. 1993.

[10] E. W. Shallenberger. 1983. 1440 Woodland Ave., Anacortes, WA 98221. Unpublished report to the Marine Mammal Commission and personal commun. 1991.

[11] J. K. Hale and C. W. Coon. 1993. Summary report - Bottomfish observer trips in the Northwestern Hawaiian Islands, October 1990 to June 1992. Pacific Area Office, Southwest Region, 2570 Dole St., Honolulu, HI 96822–2396. Unpubl. rep.

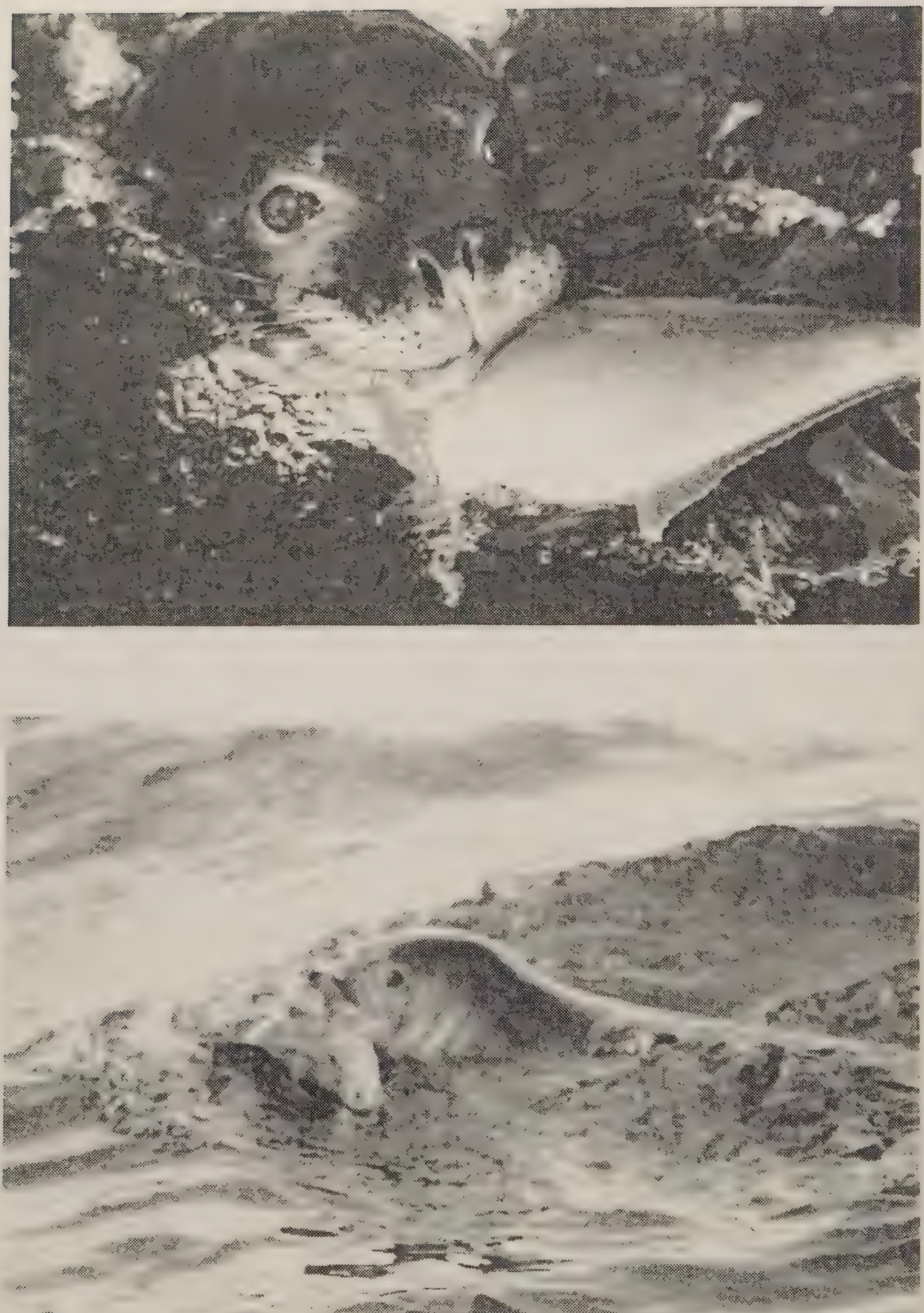

Figure 1.—Hawaiian monk seal consuming a discarded kahala (photo by Frank LaSorte, NMFS).

baited or with feathered jigs, is fished at 15–25 m. Bottlenose dolphin have been observed taking catch, but not bait or lures. Fishermen may be snagged by open hooks when dolphins take the catch and run with it.

### Trolling for Billfish and Tuna

This fishery is a sport and commercial fishery located in waters near Honolulu and along the Kona (west) coast of the Island of Hawaii. Gear involves trolling lures or live bait near the surface. Catches of both billfish (marlin and spearfish) and tuna have been reported taken by false killer whales (Zimmerman, 1983). One fisherman reported a false killer whale surfacing immediately astern of his boat holding the catch (a marlin) crosswise in its jaws (Zimmerman, 1983). Catch may either be damaged or removed from the hook entirely. Rough-toothed dolphins, bottlenose dolphins, albatrosses, and boobies have also been observed taking live bait.

### Longline Fishing for Tuna and Billfish

The Hawaiian longline fishery for broadbill swordfish has developed rapidly since 1987 when fewer than 40 vessels were in the fleet, landing less than 30,000 pounds of broadbill swordfish, a bycatch product of the tuna longline fishery. As of September 1992, the Hawaiian longline fishing fleet comprised about 165 vessels with permits, of which approximately 100 were active. Up to 40 of these vessels have been recorded as targeting broadbill swordfish in the NWHI.

The major fishing grounds for broadbills in the central Pacific region, traditionally exploited by foreign longliners, lie approximately 1,000 miles north of the Hawaiian Islands (25°–40°N.). Local longliners have fished closer to the islands, especially off the NWHI around "66 Fathom Bank" near French Frigate Shoals, St. Rogatien and Brooks Banks, and Gardner Pinnacles. A typical set consists of 16–48 km of monofilament line having as many as 700–1,000 branch (leader) lines and an equal number of hooks. The leader line is relatively short, 9–18 m long, to which is attached a "night lightstick" (a luminescent lure) about 76 cm above a broad, flat hook (8/0–9/0 Mustad). Whole squid is the preferred bait for catching broadbills. The longline is set in the evening and retrieved early the next morning.

Midwater longlines are used to catch bigeye and yellowfin tuna in the tuna longline fishery. A main line is suspended from buoys, and dropper lines are attached to the main line. Hooks are baited with whole fish of several species. Lines are usually deployed from vessels larger than 15 m. Main lines are frequently more than 32 km long with 1,000–1,400 hooks. Although yellowfin and bigeye tuna are the targeted species, swordfish, albacore, sailfish, marlin, shortbill spearfish, and sharks are often caught.

Until recently, interactions between monk seals and the longline fishery were not believed to constitute a problem in the NWHI. Events in 1990 and 1991 indicated that monk seal interactions were occurring at a level and in a manner not previously considered. Seven injured seals were observed during a survey of monk seals and turtles at French Frigate Shoals in May 1990[12]. All had head injuries ranging from abrasions to gaping wounds which could not be attributed to shark attack or harassment by adult male seals. In early 1991 nine monk seals with evidence of injury as a result of interaction with the longline fleet were reported or observed.

Sea turtle interactions with the longline fishery in the NWHI were also reported for this period. During the NMFS field surveys conducted in May 1990, a green turtle was found on Trig Island at French Frigate Shoals with monofilament line similar to longline leader protruding from its mouth.[13] Olive ridley, loggerhead, and green turtles have been reported taken on baited hooks and snagged on longline hooks in the NWHI[14], but there is some question regarding identification of the species involved. Regardless, preliminary analysis of logbook data from the Hawaii longline fishery indicates a significant take of sea turtles. For 1991, 61 total takes with 3 mortalities were reported. Leatherback turtles constituted the largest percentage of turtles taken (61%, 38 individuals) and green turtles were reported as the second highest (31%, 19 individuals)[15].

Based on logbook reports false killer whales are identified as taking catch in all pelagic longline fisheries as has been reported in other longline fisheries in the Pacific. A 1990 observer report described catch loss to a solitary killer whale, *Orcinus orca,* on one set in mid-Pacific waters (Dollar[16]). In 1991 a humpback whale was observed entangled in longline gear in the EEZ off the NWHI (Dollar[16, 17]) and a second was reported entangled in longline gear off Lanai.

From January through September 1992, longline logbook data indicated up to 68 albatrosses killed or injured over 947 reported trips. There is no distinction made in the logbooks between species of albatrosses.

### Other Fisheries

#### *Inshore Monofilament Gillnets*

Small-mesh (about 5 cm stretched mesh) gillnets are commonly set on the shallow reefs around all the main islands and allowed to soak overnight, usually in water less than 10 m depth. In 1992–93 the State of Hawaii received 288 applications for permits that listed nets as the primary gear. Gill net was specified in 161 additional applications for permits. This fishery targets inshore reef fish.

Interactions with protected species have been reported. One bottlenose dolphin calf was recovered from a gill net off Maui in 1991[18], but bottlenose dolphins are rarely reported entangled or raiding set gill nets in Hawaii; this is somewhat surprising, since they readily remove akule, opelu, bottomfish, and small tunas from handlines and trolling lines.

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[12] NMFS field survey report. May 18, 1990. Southwest Fish. Sci. Cent., Honolulu Lab., 2570 Dole St., Honolulu, HI 96822–2396.

[13] See footnote 12.

[14] NMFS longline logbook reports, 1991. Pacific Area Office, Southwest Region, 2570 Dole St., Honolulu, HI 96822–2396.

[15] See footnote 14.

[16] R. A. Dollar. 1991. Summary of swordfish longline observations in Hawaii, July 1990–March 1991. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Honolulu Lab., Southwest Fish. Sci. Cent. Admin. Rep. H-91-09, 13 p.

[17] See also footnote 11.

[18] Stranding Report ETN 91–03, Hawaii Marine Mammal Stranding Network. Pacific Area Office, Southwest Region, 2570 Dole St., Honolulu, HI 96822–2396.

There are records of spinner dolphins being taken in nets or net fragments in Hawaiian waters (Rizzuto, 1988, 1989), and there is an eyewitness account of a spinner dolphin removed from an inshore gillnet on Oahu and buried on the beach in 1990[19]. One confirmed interaction between Hawaiian monk seals and inshore monofilament gill nets has been reported from the main Hawaiian Islands. A Hawaiian monk seal was reported drowned in a gill net near Poipu, Kauai, in 1976[20]. Green turtles are periodically caught in inshore monofilament gill nets set around the main Hawaiian Islands. At least 43 (25%) and possibly as many as 86 (50%) of the 171 dead green turtles stranded in Hawaii in 1991 were likely entangled in these gill nets[21]. A hawksbill turtle was recovered from a monofilament gill net in Kaneohe Bay, Oahu, in 1977 (Balazs, 1978).

### *Lobster Fishery*

The commercial spiny lobster fishery around the main Hawaiian Islands represents a small percentage of Hawaii's total fishery. The primary commercial fishing grounds are found in the NWHI, and the fishery is governed by a Federal fishery management plan. Consistent commercial-scale operations began in the NWHI in 1976, with most vessels processing frozen lobster tails on-board and a few vessels delivering live lobster to a specialized market.

Gear used initially in the NWHI fishery was a version of the California two-chambered trap or the wooden-lath Florida pot, deployed on a main line and spaced at intervals of 2 to 10 m. Each main line had 75 to 150 traps, and vessels carried an average of 300 traps. Traps were set each day before sunset between 55 and 90 m depth, fished overnight, and retrieved the next morning. By 1985 virtually the entire fleet of 16 active vessels (compared with 4 active vessels in 1983) had converted to the black plastic crab pot which is used in the Alaska crab fisheries. This dome shaped pot is single chambered, has two entrance funnels, and can be folded in half to increase a vessel's trap carrying capacity. Between 1983 and 1985, during the conversion from the two-chambered California pot and Florida pot to the black plastic trap, the number of active vessels increased from 4 to 16 and the total trap carrying capacity of the active fleet increased from 1,200 to 12,250. From 1983 to 1990 the average trap carrying capacity of the lobster vessels in the NWHI fleet increased from 300 to over 1,000, with the number of active vessels fluctuating between 4 and 16 (Dollar and Landgraf[22]). The black plastic pots are fished in the same manner as the old traps.

A monk seal was entangled and drowned in the trap bridle and main lines of a string of lobster traps in the vicinity of Necker Island in 1986[23]. This is the only reported mortality of a Hawaiian monk seal associated with the spiny lobster fishery in the NWHI since the Crustaceans Fishery Management Plan (FMP) went into effect in 1983. In 1980 an adult leatherback turtle was entangled in a mainline of a string of lobster traps near Kure Atoll. The turtle was released alive (Humphreys[24]).

### *Miscellaneous and Unidentified Gear*

Reports between 1986 and 1992 of at least three incidents of humpback whales dragging unidentified pieces of netting around Kauai and Maui appear to demonstrate that some interaction between whales and fisheries occurs. The disposition of these animals is unknown, as are the sites where entanglements occurred. In 1992 a humpback whale mother and calf were found entangled off the east coast of the island of Hawaii in gear similar to longline deployed from shore. The animals were subsequently disentangled and released alive by the U.S. Coast Guard (ETN, personal observ.).

Green turtles have been reported hooked and entangled in the flippers and body and taken on baited hooks from shoreline pole-and-line fishermen around the main Hawaiian Islands[25]. Protected species, especially Hawaiian monk seals and often green sea turtles, are susceptible to entanglement in lost and discarded fishing equipment, including lines, nets, and other plastic flotsam. These entanglements represent secondary interactions, i.e., interactions with gear no longer actively being used, and as such are beyond the scope of this paper. However, it is often difficult to determine whether an entanglement occurred during active fishing or after the gear had been lost.

## Research

The first reports of attempts, such as shooting, to deter bottlenose dolphins from taking catch were received by the NMFS in the early 1970's. Although many methods were tried to deter predation by dolphins, none proved successful. Methods included rigging live baits with wire, hooks, or foil to confound the animals' sonar (Schlais, 1985), injecting citric acid into the baits to develop a taste aversion for certain species of fish[26], and using various noisemakers including explosive, mechanical, and electronic devices. The unconfirmed use of poisons in bait was also reported during this time. Food aversion was investigated by the NMFS in 1980[27] as a potential method of deterring cetaceans. The results proved inconclusive. Complaints to NMFS from fishermen continue and appear to peak in cycles of 3 to 5 years, covering all fisheries from longline and live bait troll fisheries for pelagic species to handlining for bottomfish and mackerel scad.

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[19] M. Hoffhines. University of Hawaii, Kewalo Basin Marine Mammal Laboratory, 1129 Ala Moana Blvd., Honolulu, HI 96814. Personal commun. 1992.

[20] Internal NMFS stranding report, March 16, 1976. Pacific Area Office, Southwest Region, NMFS, Honolulu, HI 96822–2396.

[21] G. Balazs. Southwest Fisheries Science Center, Honolulu Laboratory, 2570 Dole St., Honolulu, HI 96822–2396. Personal commun. 1991.

[22] R. A. Dollar and K. C. Landgraf. 1992. Annual report of the 1991 western Pacific lobster fishery. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Honolulu Lab., Southwest Fish. Sci. Cent. Admin. Rep. H-92-10, 26 p.

[23] NMFS lobster logbook report, November 1986. Pacific Area Office, Southwest Region, NMFS, 2570 Dole St., Honolulu, HI 96822–2396.

[24] R. L. Humphreys, Jr. 1981. Hawaiian monk seals and sea turtle — sightings and direct interactions with fishing operations in the Northwester Hawaiian Islands. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-81-6, 18 p.

[25] G. Balazs. Southwest Fisheries Science Center, Honolulu Laboratory, 2570 Dole St., Honolulu, HI 96822–2396. Personal commun. 1992.

[26] J. J. Naughton. 1981. Trip report on porpoise-, fisheries interaction, Kona, Hawaii, November 2–4, 1981. Pacific Area Office, Southwest Region, Natl. Mar. Fish. Serv., Honolulu, HI 96822–2396. Unpubl. rep. 4 p.

Sound generators were tested on pinnipeds in California and Oregon with mixed results. In some cases the acoustic harassment was successful in initially deterring pinniped predation on various species of fish. However, the animals either habituated to the sounds or ignored them (Mate and Harvey, 1987). Masking or confusing sounds proved ineffective.

Any future investigations of aversive techniques for small cetaceans will have to consider stimuli strong enough to be physically painful but not injurious, particularly under the current regulatory regime. This is particularly difficult because of the behavior and adaptability of bottlenose dolphins and perhaps other species such as false killer whales to new stimuli. The attraction for food is secondary, and the challenge or stimulus of taking fish may be the primary motivating factor for some individual animals. The use of aversive techniques may provide greater motivation for these animals to solve the "problem" or "play the game."

Other avenues of research which could be considered are the use of conspecific social sounds that indicate threat or alarm which might serve to confuse some of the more socially oriented small cetaceans and the use of pheromones as distractants.

There has been no directed investigation of alternative fishing methods or other means of reducing the potential for incidental take in Hawaii. Most of the effort to reduce incidental take of sea turtles results from regulatory actions that limit fishing effort through closed areas and limited entry and restrictions on the level of allowable incidental take. Altered fishing methods may serve to diminish seabird interactions in the longline fishery (Brothers, 1991). Setting and retrieving gear during the night, a voluntary measure taken by longline fishermen, appears to have reduced the incidental take of seabirds in this fishery.

## Management and Regulation

### Statutory and Regulatory Implications

Since 1972 various regulatory regimes have been implemented in response to fishery interactions. The Endangered Species Act of 1973 (ESA) and the Marine Mammal Protection Act of 1972 (MMPA) are the two primary Federal statutes that protect marine mammals and threatened and endangered species in Hawaiian waters, and the Migratory Bird Treaty Act of 1918 protects seabirds. The Magnuson Fishery Conservation and Management Act of 1976 (MFCMA) also provides management authority to protect these species in fisheries governed by FMP's.

The ESA prohibits the taking of endangered species except under limited circumstances. These include, but are not limited to, scientific research under permit, actions taken by personnel authorized by the NMFS or USFWS to salvage or rescue a stranded or distressed endangered animal, and an allowable level of take (except for certain marine mammals) set forth during consultation for a specific Federal activity under Section 7 of the ESA. Incidental take of listed sea turtles may be authorized, but no take can be authorized for Hawaiian monk seals or humpback whales.

The MMPA allows the incidental take of marine mammals during commercial fishing operations under certain conditions. Depleted marine mammal species, including Hawaiian monk seals, cannot be intentionally lethally taken. Under the 1988 amendments to the MMPA, some levels of mortalities of nonendangered and nondepleted marine mammals have been determined for specific fisheries. Nonlisted cetaceans may be taken incidentally or harassed, but not intentionally killed or injured, again for specific fisheries.

### Historic Context

Prior to 1988 the MMPA allowed the NMFS to issue general incidental take permits to commercial fishermen operating within the U.S. EEZ. This exception to the general moratorium on the taking of marine mammals was permitted provided that the marine mammal stocks involved were within OSP[28] levels, that the takings would not disadvantage the stocks, and that the issuance of the permits were consistent with the purposes and policies of the MMPA.

From 1981 to 1988 commercial fishermen operating in Hawaiian waters who participated in fisheries affected by small cetaceans were covered under a general permit which allowed harassment of these animals without injury or mortality. Reports of harassment were required under the permit, but few were actually received. Complaints of catch loss far exceeded reports of harassment. The high point of participation occurred in 1982 when 77 certificates of inclusion were issued to commercial fishermen allowing them to operate under the general permit. Since 1988 there have been few written reports of interactions from non-FMP regulated fisheries in Hawaii. An estimate of economic loss to the various fisheries has not been made but may be substantial in relation to the size of the fisheries.

A district court ruling in 1987 invalidated a permit issued to a Japanese fishing cooperative for the incidental taking of Dall's porpoise because species for which permits could not be issued would also be taken during fishing operations. Under this judicial interpretation NMFS could issue permits for only a few species of marine mammals for which OSP levels were known (none in Hawaii). In order to provide a temporary means of obtaining reliable information about marine mammal/ fisheries interactions, while allowing commercial fishing to continue, Congress passed the 1988 Amendments to the MMPA which established the Interim Exemption for Commercial Fisheries (Interim Exemption). Under the Interim Exemption fisheries were categorized according to the likelihood of incidentally taking marine mammals. Observer programs to monitor marine mammal interactions and reporting requirements were also established by the Interim Exemption.

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[27] B. A. Kuljis, C. S. Baker, and W. G. Gilmartin. 1981. Effects of lithium chloride on a Pacific bottlenose dolphin (*Tusiops gilli*). Presented abstract, Fourth Biennial Conference on the Biology of Marine Mammals, December 14–18, 1981, San Francisco, Calif.

[28] OSP (optimum sustainable population) as defined in the MMPA means, " . . . with respect to any population stock, the number which will result in the maximum productivity of the population or the species, keeping in mind the carrying capacity of the habitat and the health of the ecosystem of which they form a constituent element." Marine Mammal Protection Act of 1972, 86 Stat. 1027, 16 U.S.C. 1361–1407, P. L. 92–522.

All domestic Hawaiian fisheries have been classified by NMFS as Category III, with incidental takings of marine mammals unknown and/or considered extremely unlikely. This does not mean that no interactions occur, only that marine mammals would not normally be hooked, snagged, injured, or killed during fishing operations. Interactions as well as accidental lethal takes are to be reported to the NMFS.

The Interim Exemption expired 1 October 1993. The NMFS was required to develop a regime to govern the incidental taking of marine mammals associated with commercial fishing operations after 1 October 1993.

## Fishery Management Plans

Four FMP's are in effect in the U.S. EEZ around Hawaii—Precious Corals, Crustaceans, Bottomfish, and Pelagics. Protective measures for marine mammals and threatened and endangered species are generally incorporated into FMP's as they are developed. Because of concerns regarding interactions between Hawaiian monk seals and the spiny lobster fishery in the NWHI, specific conservation measures were incorporated into the Crustaceans FMP as it was being developed. These measures included closed areas within 10 fathoms of the islands in the NWHI, a 20-mile fishing refugium around Laysan Island, a trap opening size restriction of 6.5 inches, NMFS authority to place observers on lobster vessels upon request, and a protocol by which the NMFS could institute emergency protection for monk seals if a problem involving the fishery arose. Only the fishery for precious corals has not reported an interaction with marine mammals, sea turtles, or sea birds in fisheries governed by the four existing FMP's.

Section 7 consultations under the ESA for the Crustaceans, Bottomfish, and Pelagics FMP's concluded that these fisheries would not likely jeopardize the continued existence of the Hawaiian monk seal if certain gear and reporting requirements were included in the implementing regulations for these fisheries. Because of recent developments in the broadbill swordfish fishery, the Pelagics FMP is now being monitored based on Section 7 requirements. The longline fishery and bottomfish fishery are discussed together in this section because the management issues are tied to the geographic area of the NWHI and involve interactions with Hawaiian monk seals.

Allegations of Hawaiian monk seal interactions with the longline broadbill swordfish fishery in the NWHI surfaced in April 1990. NMFS field surveys in May 1990 found seven injured Hawaiian monk seals in the NWHI with possible evidence of interactions with the longline fishery. Subsequent interviews by NMFS special agents with captains and crews of 28 vessels returning from the NWHI did not generate sufficient information for enforcement action. However, there was enough consistency in reports to indicate that measures were needed to obtain definitive information on possible impacts on protected species from the longline and bottomfish fisheries.

In June 1990 the Western Pacific Fishery Management Council (Council) considered this issue. The Council proposed that NMFS implement the following: 1) A permit and logbook reporting system for the pelagic longline fishery and 2) a program to place observers on selected longline and bottomfish vessels operating in the NWHI. Although not required by regulation, observers were placed aboard one bottomfish and six longline vessels on a voluntary basis between July and October 1990 and reported interactions with sea birds, sea turtles, whales, dolphins, and monk seals. Emergency regulations were subsequently implemented by the NMFS in November 1990 restricting longline and bottomfishing operations within 50 n.mi. of selected islands in the NWHI (protected species zone). This was intended to provide a "safe zone" where Hawaiian monk seals were most likely to occur. These restrictions were waived on a trip by trip basis however, provided the operator of the vessel allowed NMFS the opportunity to place an observer aboard to document and describe interactions with protected species.

Concerns increased after further reports, in January 1991, of monk seals observed with hooks (long pieces of monofilament line attached) imbedded in their bodies and with severe injuries that appeared to be the result of interactions with fishing operations. As a result the protected species zone was expanded to include all NWHI and was closed to longline fishing in April 1991, through emergency regulation.

Amendments were subsequently implemented to both the Bottomfish FMP and the Pelagic FMP making these emergency regulations permanent. Specifically, Amendment 4 to the Bottomfish FMP restricted bottomfishing in the protected species zone which includes the area within 50 n.mi. of the islands and atolls in the NWHI from Nihoa Island to Kure Atoll. These restrictions can be waived on a trip by trip basis however, provided the operator of the vessel allows NMFS the opportunity to place an observer aboard. Amendment 3 to the Pelagics FMP prohibited fishing in the protected species zone which includes the 100 n.mi. wide corridors between islands in the NWHI where the zones are not contiguous. Logbook reporting of interactions is also required of longline vessels in order to obtain information regarding interactions outside the protected species zone.

Observer coverage became mandatory in November 1990 for bottomfish vessels because of the proximity of their fishing operations to the banks and islands of the NWHI, and the evidence of interactions between protected species and the fisheries in this area. The area from Nihoa Island to Necker Island comprises the Mau Zone. The Ho'omalu Zone is a limited entry fishing zone and comprises the area from French Frigate Shoals to Kure Island (Fig. 2). All vessels which bottomfish in either the Mau or Ho'omalu Zones are required to place onboard observer selected by NMFS. Target observer coverage is currently set at 30 percent annually.

### Future Prospects

The probable trends in protected species/fishery interactions in Hawaii are difficult to assess, but interactions will likely increase. Fishing effort is also likely to grow and place the various fish stocks under greater pressure, as an increasing human population demands more food resources. With the protection afforded by the ESA and MMPA, certain species, such as the humpback whale, will probably continue to recover from the low levels to which they were reduced by exploitation, and such increases may result in more interactions. Finally, continued environmental awareness, together with increased fishing pressure, will likely result in greater scrutiny of fisheries, resulting in more restrictions, regulations, and reporting requirements. Regardless of the difficulties in predicting trends and developing solutions for protected species/fisheries interaction problems, at the minimum, the variables that need to be monitored include population levels of the different species involved, fishing effort, and rates of interaction.

The following research and management tasks address both long- and short-term needs for the conservation and protection of marine mammals and other protected species in Hawaiian waters.

1) Accurate, timely, and consistent documentation of interactions;

2) Elimination of inshore gillnets and set nets;

3) Assessment of the status of stocks of all protected species which interact with fisheries;

4) Development of alternative fishing methods which reduce or eliminate interactions with small cetaceans; and

5) Where interactions cannot be eliminated or mitigated by other means, development of management schemes which allow for incidental take of selected species of marine mammals in Hawaiian waters provided that the stocks of marine mammals are not adversely affected.

Many of the tasks identified above rely upon the cooperation of a number of agencies and will be affected by the restrictions and requirements of the applicable Federal and state statutes. Given the biology of the protected species involved in fishery interactions, the current and likely future regulatory regimes, and the nature and locations of the Hawaiian fisheries, the interaction problems identified ultimately may have no legal or practical solutions.

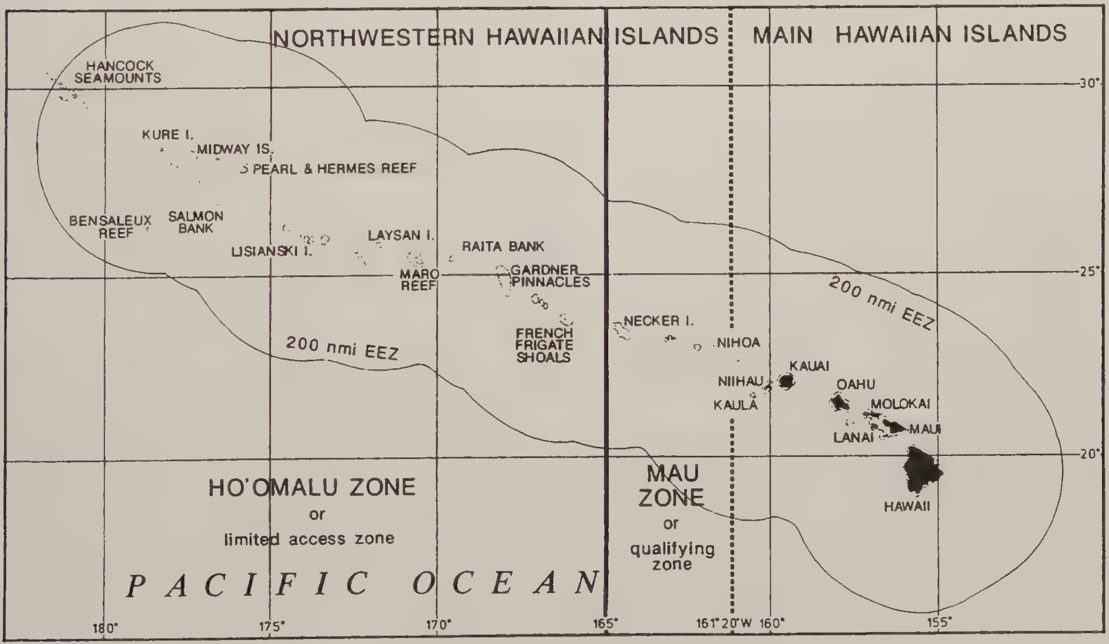
NORTHWESTERN HAWAIIAN ISLANDS
MAIN HAWAIIAN ISLANDS
HANCOCK SEAMOUNTS
KURE I.
MIDWAY IS.
PEARL & HERMES REEF
BENSALEUX REEF
SALMON BANK
LISIANSKI I.
LAYSAN I.
RAITA BANK
MARO REEF
GARDNER PINNACLES
FRENCH FRIGATE SHOALS
NECKER I.
NIHOA
KAUAI
NIIHAU
KAULA
OAHU
MOLOKAI
LANAI
MAUI
HAWAII
200 nmi EEZ
200 nmi EEZ
HO'OMALU ZONE
or
limited access zone
MAU ZONE
or
qualifying zone
PACIFIC OCEAN
30°
25°
20°
180°
175°
170°
165°
161°20'W
160°
155°

Figure 2.—Northwestern Hawaiian Islands bottomfish management areas.

## Acknowledgments

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# Chromatophoromas and Chromatophore Hyperplasia in Pacific Rockfish (*Sebastes* spp.)[1]

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## ABSTRACT

**Pacific rockfish from Cordell Bank, off central California (United States), were collected and histologically examined from 1985 to 1990. Hyperplastic and neoplastic cutaneous lesions, involving dermal chromatophores, were observed in five species; yellowtail rockfish (*Sebastes flavidus*), bocaccio (*S. paucispinis*), olive rockfish (*S. serranoides*), widow rockfish (*S. entomelas*), and chilipepper rockfish (*S. goodei*). Yearly prevalences were highest in *S. paucispinis* (29–38%). Prevalence was initially low in *S. flavidus*, but increased more than 3-fold from 1985 (7.5%) to 1990 (25%). The majority of lesions were black, but white, yellow, orange, red, and mixed-color variants were also seen. Lesions were found in skin, fins, lips, gingiva, tongue, urogenital papilla, conjunctiva, and cornea of the eye. Flat lesions were consistent with melanophore (black), xanthophore (yellow or orange), and erythrophore (red) hyperplasia. Neoplastic lesions included melanophoromas, amelanotic melanophoromas, xanthophoromas, erythrophoromas, and mixed chromatophoromas. Although etiology has not been determined, interest is currently focused on potential exposure to chemical and radioactive carcinogens from the Farallon Island Radioactive Waste Dump, 30 km to the south.**

## INTRODUCTION

Pacific rockfish (*Sebastes spp.*) are long-lived (some with life spans in excess of 100 years), ovoviviparous marine fish belonging to the family *Scorpaenidae* (1). *Sebastes* is the most common genus found off the North American Pacific coast, and it inhabits a variety of ecosystems ranging from shallow coastal kelp beds to offshore reefs in 750 m of water (2, 3). A popular food fish, they are extensively harvested by both commercial and sport fishermen.

One of the most prolific fishing grounds off central California (United States) is Cordell Bank. Cordell Bank is the northernmost sea mount in the California continental shelf and is located 80 km northwest of San Francisco (Fig. 1). The bank has been the primary site of ongoing rockfish recruitment studies by the Tiburon Laboratory (Tiburon, CA) of the National Marine Fisheries Service. Over the course of numerous sampling trips, pigmented lesions consistent with chromatophore hyperplasia and neoplasia (chromatophoromas) were observed in five species of rockfish: yellowtail rockfish (*S. flavidus*); bocaccio (*S. paucispinis*); olive rockfish (*S. serranoides*); widow rockfish (*S. entomelas*); and chilipepper rockfish (*S. goodei*).

Chromatophoromas are cutaneous pigment cell tumors that arise from dermal chromatophores normally present in the skin of fish, amphibians, and reptiles (4–6). The four chromatophore types commonly found in fish skin are melanophores with black or brown pigment (melanin), iridophores with colorless pigments (purines), erythrophores with red pigments, and xanthophores with yellow pigments. Xanthophores and erythrophores are closely related and both contain carotenoids, pteridines, and flavins. Orange chromatophores are arbitrarily classified as either xanthophores or erythrophores, depending on which cell type they most closely resemble.

Chromatophoromas are common tumors of fish, and large epizootics have been reported in both marine and freshwater environments. Marine species involved with chromatophoroma epizootics include croakers (*Nibea mitsukurii*) off the Pacific coast of Japan (7), deepwater redfish (*Sebastes mentella*) in the North Atlantic (8), and butterflyfish (*Chaetodon multicinctus* and *C. miliaris*) from the Hawaiian Islands (9). Freshwater epizootics have involved drum (*Aplodinotus grunniens*) from the Great Lakes[3] and domestic goldfish (*Carassius auratus*) (10, 11).

The purpose of this study was to characterize the gross, histological, and electron microscopic features associated with hyperplastic and neoplastic pigmented lesions found in Pacific rockfish from Cordell Bank and to assess prevalence with respect to year, species, sex, age, and lesion type.

## MATERIALS AND METHODS

**Sampling.** Rockfish from Cordell Bank were collected on a monthly basis, with some interruptions, from 1985 to 1990. Fish were located in the water column using an electronic fish finder and were caught using a hook-and-line technique. Sampling was biased toward mature female *S. flavidus* (collected for another study), but sex, age, number, and species varied with depth of fishing and time of year.

**Scoring of Lesions.** All *S. flavidus*, *S. paucispinis*, *S. entomelas*, and *S. goodei* with and without pigmented skin lesions were scored by a standardized method. The scoring sheet consisted of detailed drawings of the right and left sides of the fish. Drawings were divided into four quadrants based on a horizontal line drawn from the nose through the middle of the tail and a second vertical line extending from a point midway between the fifth and sixth dorsal spines down to the ventral body wall. Lesions were copied onto individual drawings, and each quadrant was subjectively scored on a scale of 1–6 based on the degree of black pigmentation and neoplastic development (1 = normal skin; 2–5 = mild to severe melanosis; 6 = raised black tumor).

Yellow or orange (xanthophore) and red (erythrophore) lesions were scored separately on a simplified basis of color, location, and number.

**Statistical Analyses.** Nonparametric tests were applied to prevalence and scoring data using the Number Cruncher Statistical System, version 5.03. Analyses were performed for *S. flavidus* and *S. paucispinis* where sample size was sufficiently large. Prevalence was tested using $\chi^2$ analyses for differences between years, species, sexes, ages, and lesion types. Lesion scores were evaluated using the Kruskal-Wallis test for differences between years, species, sexes, and ages. Differences in lesion scores between dorsal and ventral, anterior and posterior were also compared using the Wilcoxon matched pairs test.

**Gross Examination, Tissue Fixation, and Processing.** Standard length, total wet weight, sex, and age (based on otolith examination) were determined, and complete necropsy was performed on representative fish. Tissues for light microscopy were fixed in 10% buffered formalin, and some were demineralized in formic acid. Light microscopy tissues were routinely paraffin processed, sectioned at 5–7 µm, and stained with hematoxylin and eosin. Tissues for transmission electron microscopy were either fixed in half-strength Karnovsky's solution or were subsampled from formalin-fixed tissues. EM[4] tissues were processed and embedded in epon, semithin-sectioned at 1 µm, and stained with toluidine blue. Following an initial screen of semithin sections, selected

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[2] To whom requests for reprints should be addressed.

[3] M. S. Okihiro and P. C. Baumann, U. S. Fish and Wildlife Service, Columbus, OH, unpublished data.

[4] The abbreviations used are: EM, electron microscopy; FIRWD, Farallon Island Radioactive Waste Dump.

blocks were sectioned at 800–900 Å, stained with 2% uranyl acetate and Reynolds' lead citrate, and viewed with a Zeiss 10 or Phillips 410 electron microscope.

## RESULTS

### Prevalence

Prevalence data on *S. flavidus* reflect the full 6 years of the study (1985–1990). Prevalence data were determined for 4 years (1985–1988) for *S. paucispinis* and *S. entomelas* and were compiled for 2 years (1985–1986) for *S. goodei*. No prevalence data were obtained for *S. serranoides*. Yearly prevalences were consistently higher in *S. paucispinis* compared to all other species and were significantly ($P < 0.0001$) higher than lesion prevalence in *S. flavidus* (Table 1). Although lesion prevalence peaked in 1987 at 38.6%, there were no significant ($P = 0.1875$) differences between years in *S. paucispinis*. Prevalence in *S. flavidus* was initially low but has significantly ($P < 0.0001$) increased from 1985 (7.5%) to 1990 (25%).

Melanophore lesions (both hyperplastic and neoplastic) were the most common lesion type found in *S. flavidus*, and prevalences were significantly ($P < 0.0001$) higher than the combined total of xanthophore and erythrophore lesions in every year of the study (Table 2). No seasonal pattern was determined, but yearly prevalences followed the same general pattern of decreasing prevalence from melanophore to xanthophore to erythrophore lesions. The prevalences of melanophore lesions, melanophoromas, and combined xantho/erythrophore lesions were all significantly ($P < 0.0001$) higher in 1990 compared to earlier years. The prevalence of melanophoromas and xantho/erythrophore lesions was probably underestimated during the first year of the study, and no attempt was made to determine prevalence of xanthophore or erythrophore tumors.

The prevalence of melanophore lesions, melanophoromas, and xantho/erythrophore lesions increased significantly ($P < 0.0001$) with age in *S. flavidus* (Table 3). The increase was most prominent with melanophore lesions (1.3%, 1–10-year group; and 66.7%, >40-year group). Similar patterns of higher prevalences of melanophore lesions in older fish were also observed with *S. paucispinis*, *S. entomelas*, and *S. goodei*, but sample sizes of older fish were insufficient to test statistically.

Table 1 *Prevalence of pigmented skin lesions in S. flavidus, S. paucispinis, S. entomelas, and S. goodei collected from Cordell Bank from 1985 to 1990*

| | % prevalence (no. fish with lesions/no. fish examined) | | | |
|---|---|---|---|---|
| Year | *S. flavidus* | *S. paucispinis* | *S. entomelas* | *S. goodei* |
| 1985 | 7.5% (7/94) | 35.1% (13/37) | 6.3% (1.16) | 8.2% (4/49) |
| 1986 | 11.3% (15/133) | 29.0% (11/38) | 5.3% (1/19) | 16.7% (3/18) |
| 1987 | 9.8% (15/153) | 38.6% (17/44) | 0.0% (0/8) | ND |
| 1988 | 11.0% (12/109) | 37.8% (14/37) | 0.0% (0/2) | ND |
| 1989 | 16.8% (17/101) | ND[a] | ND | ND |
| 1990 | 25.5% (56/220) | ND | ND | ND |

[a] Not done.

Table 2 *Prevalence of pigmented skin lesions in S. flavidus collected from Cordell Bank from 1985 to 1990*

| | % prevalence (no. fish with lesions/no. fish examined) | | |
|---|---|---|---|
| Year | Melanophore lesions | Melanophormoas | Xantho/erythrophore lesions |
| 1985 | 7.5% (7/94) | 0.0% (0/94) | 0.0% (0/94) |
| 1986 | 9.8% (13/133) | 1.5% (2/133) | 2.3% (3/133) |
| 1987 | 6.5% (10/153) | 1.3% (2/153) | 3.3% (5/153) |
| 1988 | 9.2% (10/109) | 0.9% (1/109) | 1.8% (2/109) |
| 1989 | 15.8% (16/101) | 2.0% (2/101) | 2.0% (2/101) |
| 1990 | 22.7% (50/220) | 8.6% (19/220) | 11.4% (25/220) |

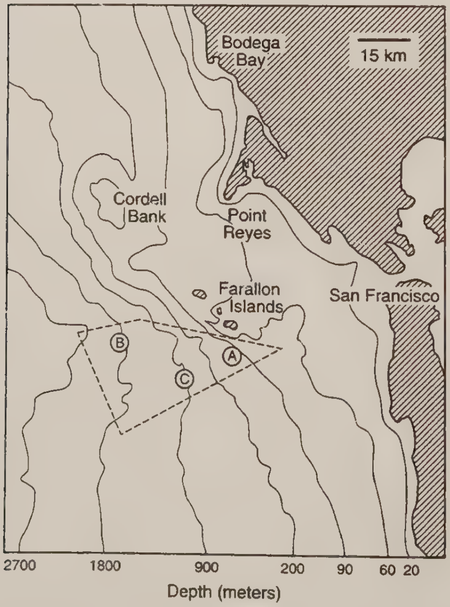

Fig. 1. The study site was located at Cordell bank, 80 km northwest of San Francisco. Farallon Islands Radioactive Waste Dump is delineated by *dashed lines*; *A, B*, and *C*, specific disposal sites in 90, 1800, and 900 m of water.

Prevalence of melanophore lesions and melanophoromas was consistently higher in male *versus* female *S. flavidus* in almost all age groups. The difference was not significant, however ($P = 0.483$), and there was little difference in prevalence of xantho/erythrophore lesions between sexes in *S. flavidus*. There was also no significant difference in melanophore lesion prevalence between sexes in *S. paucispinis*. The prevalence of melanophore lesions was three times higher in male (23.1%) *versus* female (7.4%) *S. goodei*, and both *S. entomelas* with lesions were female. Sample sizes of *S. goodei* and *S. entomelas* were insufficient, however, to test statistically.

An extensive survey of the U.S. Pacific coast was not conducted, but periodic port sampling of trawl catches in Oregon and Washington by National Marine Fisheries Service personnel over the past 6 years has revealed only occasional rare *S. flavidus* with chromatophore lesions.[5]

### Scoring

Scoring data from 106 *S. flavidus*, 45 *S. paucispinis*, 2 *S. entomelas*, and 7 *S. goodei* with melanophore lesions were evaluated based on age and sex. The average melanophore lesion score for all age groups was significantly ($P < 0.001$) higher in *S. flavidus* (19.8) compared to *S. paucispinus* (10.8). Average scores for *S. flavidus* increased significantly ($P < 0.0001$) with age (9.3, 1–10-year group; 25.0, >40-year group) (Table 4). Male *S. flavidus* scored consistently higher than females in all age groups, and the overall melanophore lesion score was significantly higher ($P < 0.001$) in males (24.3) than females (17.4). In contrast, there were minimal differences in lesion scores between male and female *S. paucispinis* or *S. goodei* and no appreciable change in lesion scores as these fish grew older.

Evaluation based on lesion distribution revealed that melanophore lesions in *S. flavidus* were significantly ($P = 0.0001$) more severe dorsally (10.3 dorsal and 9.4 ventral). Anterior scores (10.2) were

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[5] M. Eldridge, National Marine Fisheries Service, Southwest Fisheries Science Center, Tiburon, CA, personal communication.

Table 3 *Age distribution of S. flavidus with respect to percentage prevalence (no. fish with lesions/no. fish examined) of melanophore lesions, melanophoromas, and xantho/erythrophore lesions*

| | Age in years | | | | |
|---|---|---|---|---|---|
| Lesion type | 1–10 | 11–20 | 21–30 | 31–40 | >40 |
| Melanophore lesions | 1.3%<br>(3/225) | 7.3%<br>(25/344) | 31.0%<br>65/210) | 44.0%<br>(11/25) | 66.7%<br>(2/3) |
| Melanophoromas | 0%<br>(0/225) | 0.6%<br>(2/344) | 10.0%<br>(21/210) | 7.0%<br>(2/25) | 33.3%<br>(1/3) |
| Xantho/erythrophore lesions | 1.8%<br>(4/225) | 3.2%<br>(11/344) | 9.0%<br>(19/210) | 8.0%<br>(2/25) | 33.3%<br>(1/3) |

Table 4 *Age and sex distribution of S. flavidus with respect to average melanophore lesion score*

| | Age in years | | | | |
|---|---|---|---|---|---|
| *S. flavidus* | 1–10 | 11–20 | 21–30 | 31–40 | >40 |
| All fish | 9.3 | 14.2 | 21.8 | 22.6 | 25.0 |
| Males | NA[a] | 16.2 | 25.5 | 25.8 | 41.0 |
| Females | 9.3 | 13.6 | 19.9 | 20.0 | 9.0 |

[a] Not applicable.

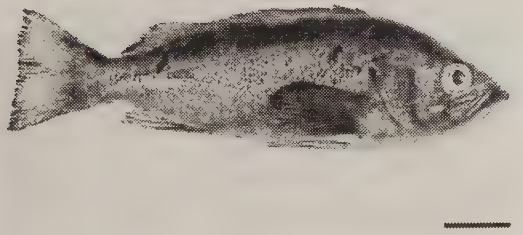

Fig. 2. *S. flavidus* with mild melanophore hyperplasia. *Bar* = 5 cm.

higher than posterior (9.6), but the difference was not as significant ($P = 0.1005$). The most severely affected quadrant was the dorsal-anterior (5.3), and the least affected was the ventral-posterior (4.5). Melanophoromas in *S. flavidus* also tended to occur dorsally (62 dorsal, 45 ventral) and cranially (60 anterior, 47 posterior). Again the most severely affected quadrant was the dorsal-anterior (34 tumors), and the least affected was the ventral-posterior (19 tumors).

## Gross Pathology

*S. flavidus* (810 specimens), *S. paucispinis* (156 specimens), *S. entomelas* (45 specimens), *S. goodei* (67 specimens), and *S. serranoides* (5 specimens) with and without pigmented skin lesions were examined grossly.

**Normal Pigmentation.** *S. flavidus* without lesions were dark gray to greenish brown dorsally, with lighter colored flanks and a pale ventrum. There were often light grey to white patches at the base of the dorsal fin and small, indistinct, red-brown spots over the flanks. Fins (especially caudal) were yellow.

**Melanophore Lesions.** Black pigmented lesions in *S. flavidus* were found in the skin, fins, lips, gingiva, tongue, urogenital papilla, conjunctiva, and cornea of the eye. The smallest lesions were 0.1–2.0 cm in diameter, round to irregular flat foci (Fig. 2). In severely affected fish, foci coalesced to form large areas of melanosis covering up to 80% of skin and fins (Fig. 3). The surface of the smallest lesions was usually smooth, but larger lesions were often rough, with irregular displacement of scales. On section, foci and areas of melanosis were restricted to the skin.

Raised black masses varied from 0.2 to 2.0 cm in diameter and were usually sessile, broad based, and nonencapsulated (Fig. 4). Although some masses arose in areas of normal pigmentation, the majority were centered within larger areas of melanosis. Some black tumors had central regions that were opaque white (Fig. 5) or were mixed with yellow and/or orange tissue. Large masses occasionally extended through the dermis into the underlying subcutaneous tissue.

Pigmented lesions in *S. serranoides* and *S. entomelas* were similar to those in *S. flavidus*, with affected fish having a range of lesions from small foci of melanosis to large black tumors. Lesions in *S. paucispinis* (Fig. 6) and *S. goodei* were limited to irregular, flat foci and areas of melanosis.

**Xanthophore and Erythrophore Lesions.** Hyperplastic (flat) and neoplastic (raised) yellow, orange, and red lesions were seen only in *S. flavidus* and, although much less common, were similar in distribution and gross morphology (except for color) to melanophore le-

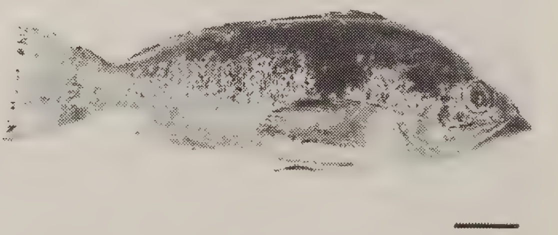

Fig. 3. *S. flavidus* with severe melanophore hyperplasia. *Bar* = 5 cm.

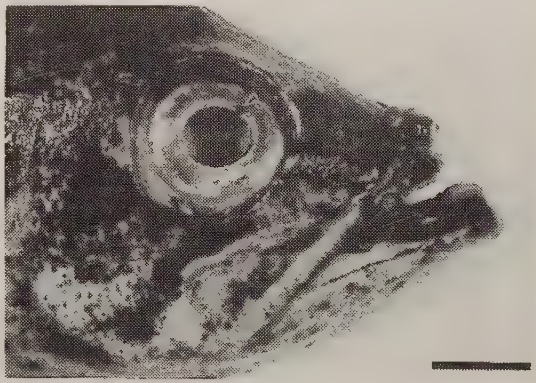

Fig. 4. *S. flavidus* with severe melanophore hyperplasia involving the entire head, focal melanophore hyperplasia in the cornea (*arrowhead*), and melanophoroma over the nose. *Bar* = 2 cm.

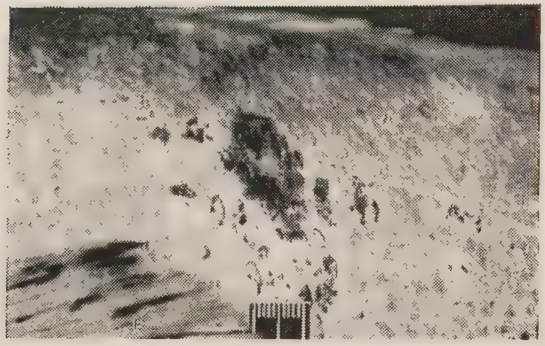

Fig. 5. *S. flavidus* with melanophore hyperplasia involving the pectoral fin (*F*) and melanophoroma with central depigmentation over the flank. *Scale* = 10 mm.

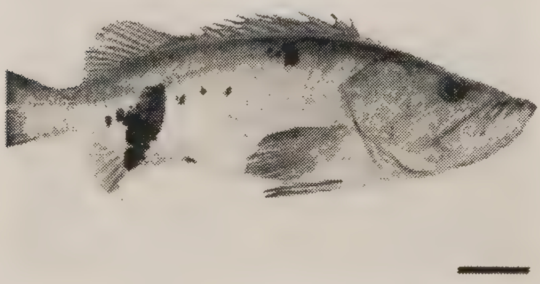

Fig. 6. *S. paucispinis* with multiple areas of melanophore hyperplasia. *Bar* = 10 cm.

sions. Orange lesions, often seen with yellow lesions, were closer in color to yellow than red. Red lesions were distinct with respect to color and rare.

**Internal Organs.** *S. flavidus* often had multiple, 1–6-mm-diameter, grey, firm, nodular masses in the kidneys, spleen, mesenteries, and occasionally the liver. A few *S. flavidus* with melanophoromas had multiple, 0.25–1.5-cm-diameter, translucent white to black, nodular masses in the liver. One *S. serranoides* with multiple melanophoromas had two nodular gill masses.

### Histopathology

Cutaneous lesions were histologically examined from 32 *S. flavidus* and included 42 melanophore lesions, 7 xanthophore (2 yellow and 5 orange) lesions, 4 erythrophore (red) lesions, and 8 mixed melanoxanthophore (black mixed with yellow and/or orange) lesions. Melanophore lesions were also collected from 2 *S. paucispinis* and one *S. serranoides*. For comparison, skin (dorsal and flank) and fins (pectoral and caudal) from 3 *S. flavidus* without lesions were also examined.

**Normal Pigmentation.** Pigment cells in normal *S. flavidus* skin were present in four distinct dermal layers: (*a*) in the stratum spongiosum at the dermal-epidermal junction; (*b*) between the stratum spongiosum and scales; (*c*) between the scales and stratum compactum; and (*d*) between the stratum compactum and subcutaneous fat. Melanophores were present in all four layers and were arranged into single, sometimes discontinuous rows of spindle cells packed with granular black-brown pigment. There were proportionally more melanophores in superficial *versus* deep layers and in dorsal *versus* flank skin. Scattered throughout all layers were small numbers of finely tapered spindle cells, devoid of melanin (presumptive xanthophores). Some presumptive xanthophores contained small, clear to pale yellow, intracytoplasmic vacuoles.

In the fins, dermal chromatophores were reduced to a single, irregular, discontinuous layer adjacent to the dermal-epidermal junction. In areas where scales were present (primarily in the caudal fin), scattered chromatophores were also found in the stratum spongiosum adjacent to scales. In contrast to the skin, there were relatively few melanophores in the fins and proportionally greater numbers of presumptive xanthophores. Of the two fins examined, there were far fewer melanophores in the caudal fin.

**Melanophore Lesions.** The smallest foci of melanosis in the skin and fins of *S. flavidus* were characterized by hyperplasia of dermal melanophores in the most superficial layer of chromatophores, adjacent to the epidermis. Hyperplastic melanophores were heavily pigmented and densely packed into multiple layers. Melanophore hyperplasia varied from mild (Fig. 7) to severe (Fig. 8) and was restricted to the dermis. The epidermal stratified squamous epithelium was often hyperplastic and sometimes contained increased numbers of mucous and/or mononuclear inflammatory cells (primarily lymphocytes). Foci and areas of melanosis in *S. paucispinis* and *S. serranoides* were histologically similar to those in *S. flavidus*.

Areas of severe melanophore hyperplasia in *S. flavidus* often graded into small foci of dysplasia and early neoplasia. Neoplasms were classified as melanophoromas and were distinguished from hyperplastic foci by their accentuated disorganization, variability in pigmentation, and pleomorphism (Fig. 9). It was difficult to reliably predict histological appearance based on gross morphology, and many flat foci of apparent benign melanosis were later shown to be neoplastic.

All melanophoromas were composed of pleomorphic populations of stellate to spindle cells arranged into tightly packed, interweaving fascicles and whorling bundles (Fig. 10). The majority of tumors were well vascularized, and, in some, there was whorling of spindle cells around individual capillaries. Spindle cells had indistinct borders and varied from elongate and finely tapered to plump with abundant cytoplasm. Degree of pigmentation was highly variable, with some cells having only a fine dusting of granular black-brown pigment while others were packed with melanin. In some areas, tumor cells were completely devoid of pigment (Fig. 11), and even the most heavily melanized tumors were usually a mixture of pigmented and nonpigmented cells. Nuclei were oval to elongate, and although mitotic figures were usually rare, a few tumors had mitotic indices as high as 3–5 per 40× objective field. Grossly white tumors, classified

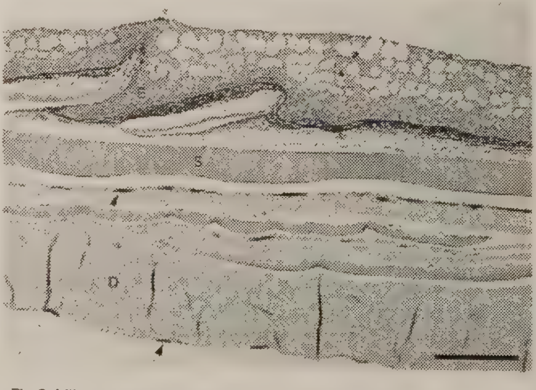

Fig. 7. Mild melanophore hyperplasia in the superficial dermis, adjacent to the epidermis (*E*), of *S. flavidus*. Normal melanophore layers (*arrowheads*) are located below the scale (*S*) and the stratum compactum of the dermis (*D*). H&E. *Bar* = 200 μm.

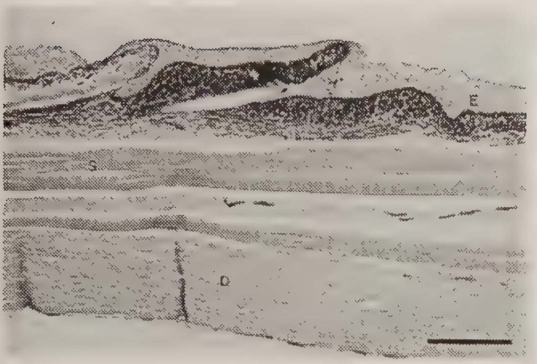

Fig. 8. Severe melanophore hyperplasia in *S. flavidus*. Hyperplasia is limited to the superficial dermis, adjacent to the epidermis (*E*). Normal melanophore layers below the scale (*S*) and stratum compactum of the dermis (*D*) are not involved. H&E. *Bar* = 200 µm.

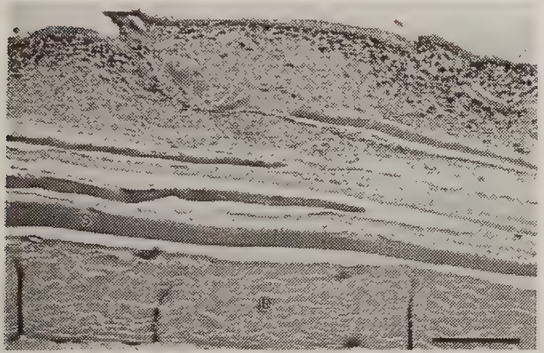

Fig. 9. Early melanophoroma in *S. flavidus*. Neoplastic melanophores are pleomorphic, variably pigmented, and arranged into irregular tightly fascicles but are still resticted to the superficial dermis above the scale (*S*) and stratum compactum of the dermis (*D*). H&E. *Bar* = 200 µm.

as amelanotic melanophoromas, were primarily composed of nonpigmented spindle cells, but almost all had small foci of melanin-bearing cells.

Small melanophoromas were restricted to the superficial dermis, but with increasing size there was a progressive extension through the stratum compactum and occasional invasion of the subcutis. Fin tumors often eroded into bony fin rays, and extensive invasion frequently resulted in severe bone destruction and variable new periosteal bone formation. Reactive bone formation was also occasionally seen in scales isolated by tumor cells.

The majority of melanophoromas were infiltrated with moderate to large numbers of lymphocytes, and many contained large macrophage aggregates packed with melanin (Fig. 10). The overlying epidermis was often eroded or ulcerated and infiltrated with lymphocytes and macrophages. All black-and-white lesions were negative for reflecting platelets (characteristic of iridophores) when examined with polarized light. Melanophoromas and amelanotic melanophoromas were also found in *S. serranoides* and were identical to those in *S. flavidus*.

**Xanthophore and Erythrophore Lesions.** Nonraised yellow, orange, and red lesions in *S. flavidus* were difficult to detect and interpret with routine histological processing. Alcohol dehydration resulted in the extraction of fatty carotenoid pigments, and presumptive xanthophores and erythrophores were almost indistinguishable from other spindle cells normally present in the dermis. Some xanthophores were identified by the presence of clear to pale yellow intracytoplasmic vacuoles, but in general, hyperplastic foci involving these cells could not be reliably diagnosed with hematoxylin and eosin-stained paraffin sections.

Mass lesions, involving xanthophores (xanthophoromas) and erythrophores (erythrophoromas), were not histologically distinguishable either from each other or from amelanotic melanophoromas in routine hematoxylin and eosin sections. All three tumor types were composed of finely tapered spindle cells devoid of melanin. Because of this, the classification of tumors was primarily based on coloration prior to fixation. Yellow and orange tumors were classified as xanthophoromas, and red tumors were identified as erythrophoromas. Tumors with more than one color (usually black and yellow) were classified as mixed chromatophoromas.

The only way to reliably evaluate yellow, orange, and red lesions histologically was via EM semithin sections. Toluidine blue-stained semithin sections revealed the presence of small to large amounts of distinct green lipid droplets within presumptive xanthophores and

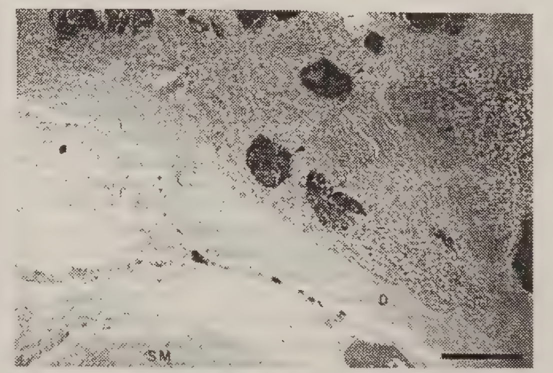

Fig. 10. Advanced melanophoroma in *S. flavidus*. The tumor, composed of heavily pigmented spindle cells arranged into densely packed fascicles, has invaded the stratum compactum of the dermis (*D*) but not the underlying skeletal muscle (*SM*). Numerous large aggregates of melanin laden macrophages (*arrowheads*) are present. H&E. *Bar* = 500 µm.

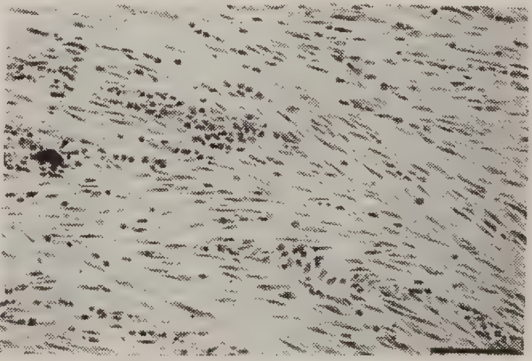

Fig. 11. Amelanotic portion of an advanced melanophoroma in *S. flavidus*. Except for a single melanophore (*arrowhead*), interweaving fascicles of neoplastic spindle cells are devoid of pigment. H&E. *Bar* = 50 µm.

erythrophores. All yellow, orange, and red lesions were negative for reflecting platelets when examined with polarized light.

**Internal Organs.** Nodular grey masses found in the internal organs of many *S. flavidus* were identified as foci of cartilaginous metaplasia in response to chronic *Ichthyophonus sp.* infection. Liver masses from one *S. flavidus* were consistent with metastasis from one of several cutaneous melanophoromas. The masses, composed of plump nonpigmented spindle cells, were found throughout the hepatic parenchyma and within blood vessels. The two gill masses from one *S. serranoides* were also believed to represent metastatic lesions from a cutaneous melanophoroma. The gill masses were somewhat pleocellular, but both were in part composed of nonpigmented spindle cells arranged into fascicles or whorling bundles.

### Electron Microscopy

EM tissues were collected from 12 *S. flavidus* with lesions and included 2 foci of melanophore hyperplasia, 9 melanophoromas, one amelanotic melanophoroma, 2 xanthophoromas, one focus of erythrophore hyperplasia, one erythrophoroma, and 2 mixed (melano-xanthophore) chromatophoromas. For comparison, EM sections of skin (dorsal and flank) and fins (pectoral and caudal) from three *S. flavidus* without lesions were also examined.

**Normal Pigmentation.** Normal melanophores in the skin and fins were characterized by smooth cell membranes with few pinocytotic vesicles, small numbers of mitochondria, small to moderate amounts of ER, and large numbers of membrane-bound, electron-dense, round to oval melanosomes. Melanosomes were evenly distributed throughout the cytoplasm and varied from 0.2 to 0.6 μm in diameter. Xanthophores in normal skin and fins were similar ultrastructurally except for the absence of melanosomes and the presence of small to moderate amounts of cytoplasmic lipid. The lipid was randomly distributed, and pterinosomes were not observed.

**Melanophore Lesions.** Both melanophore hyperplasia and neoplasia were characterized by pleomorphic stellate to spindle cells with variable numbers of electron-dense melanosomes ranging from 0.15 to 0.60 μm (Fig. 12). Mixed in were some cells with lipid droplets and others with membrane-bound organelles intermediate in electron density to fat and melanin. Mitochondria were often distorted, and ring forms were common. Irregular membrane fragments and myelin figures were often seen both within and between cells. Nuclei were pleomorphic, and pinocytotic vesicles were common. One melanophoroma had widely scattered iridophores characterized by an empty latticework of membranes resulting from the dissolution of reflecting platelets during processing. The amelanotic melanophoroma was predominantly composed of spindle cells completely devoid of pigment.

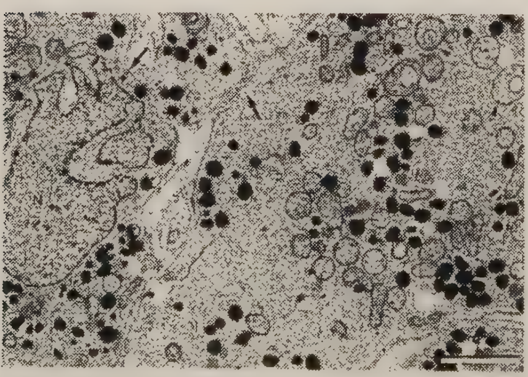
Fig. 12. Malignant melanophores with pleomorphic nuclei (*N*), scattered electron-dense melanosomes, dysplastic ring-shaped mitochondria (*arrowheads*), and numerous pinocytotic vesicles along cell margins (*arrows*). Uranyl acetate and lead citrate. *Bar* = 2 μm.

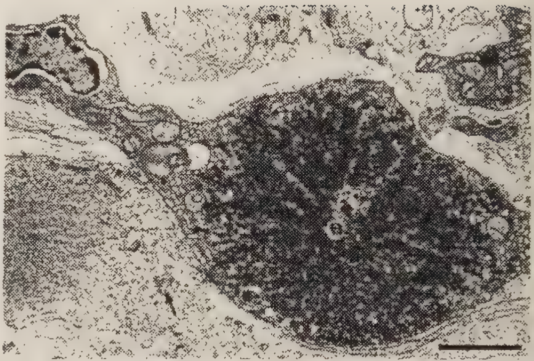
Fig. 13. Malignant xanthophore packed with lipid droplets arranged in radial fashion around a central focus of filaments. Adjacent cell contains several Golgi complexes (*arrowhead*), myelin figures (*arrow*), and lipid that is less electron dense. Uranyl acetate and lead citrate. *Bar* = 2 μm.

**Xanthophore and Erythrophore Lesions.** The two xanthophoromas examined differed markedly ultrastructurally. The first was characterized by pleomorphic spindle cells packed with lipid droplets (0.03–0.30 μm) which were often radially arranged around a central focus of filaments (Fig. 13). The second xanthophoroma had almost no lipid but was instead composed of cells filled with pterinosomes and large numbers of pinocytotic vesicles (Fig. 14). Pterinosomes ranged from 0.3 to 0.7 μm and were filled with amorphous flocculent material and disorganized fibrils. The second xanthophoroma also contained scattered iridophores.

The focus of erythrophore hyperplasia was characterized by large polygonal cells packed with lipid. The majority of lipid was in the form of small (0.01–0.05 μm) round droplets, but in some cells there was coalescence into large irregular "lakes" of fat up to 4 μm in diameter. The erythrophoroma contained few cells with lipid and was largely composed of nonpigmented cells with variable amounts of intermediate filaments, polyribosomes, and rough endoplasmic reticulum (Fig. 15).

Mixed chromatophoromas were characterized by the presence of both melanophores with melanosomes and presumptive xanthophores with variable amounts of lipid. No viral particles were seen in any of the tissue examined.

## DISCUSSION

The gross, histological, and electron microscopic features of pigmented cutaneous lesions in Pacific rockfish are all consistent with the diagnosis of chromatophore hyperplasia and neoplasia. Although it has been proposed that these tumors be called chromatoblastomas (12), because of the evidence that all chromatophores arise from a neural crest-derived, pluripotent stem cell (*i.e.*, chromatoblast), we prefer to identify these tumors as chromatophoromas because the majority do show varying degrees of differentiation with respect to specific pigment cell types.

Subclassification of chromatophoromas is primarily based on the identification of specific pigment organelles (*e.g.*, melanosomes with melanophoromas or reflecting platelets with iridophoromas), but difficulty can arise when trying to differentiate xanthophore from erythrophore lesions because these cell types share many of the same pigments and pigment organelles. Our EM findings reflected this

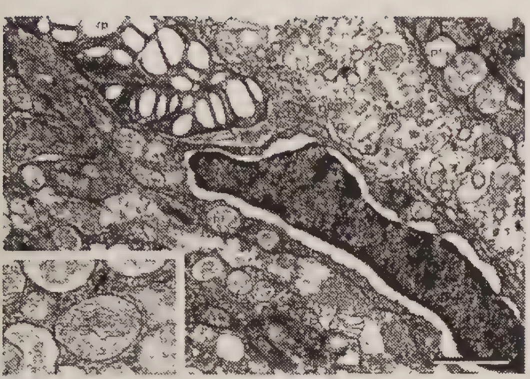

Fig. 14. Malignant xanthophores and one iridophore. Reflecting platelets (*rp*) in the iridophore were dissolved out during processing, leaving behind an empty latticework of empty membranes. Xanthophores contain numerous vesicles and pterinosomes (*pt*). Uranyl acetate and lead citrate. *Bar* = 1 µm. *Inset*, pterinosome with disorganized meshwork of fibrils.

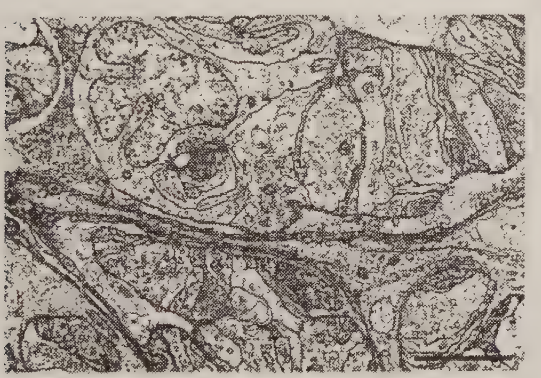

Fig. 15. Malignant erythrophores, with scattered filaments and small vesicles, are completely devoid of pigment. Uranyl acetate and lead citrate. *Bar* = 2 µm.

because although we did demonstrate organelles (pterinosomes and presumptive carotenoid lipid droplets) typical of both xanthophores and erythrophores, there was no consistency with respect to ultrastructure, and subclassification was therefore made on the basis of gross coloration.

Hyperplastic lesions are likely precursors to chromatophoromas in at least 3 of 5 species (*S. flavidus*, *S. serranoides*, and *S. entomelas*). Progression appears to occur stepwise from mild to severe hyperplasia, dysplasia, and eventual neoplasia. While the majority of chromatophoromas were benign and restricted to the dermis, some of the largest were malignant as evidenced by increasing anaplasia, invasion, and occasional metastasis to liver (in *S. flavidus*) or gill (in *S. serranoides*). Anaplastic chromatophoromas were quite variable histologically and, with severe pigment loss, must be differentiated from other cutaneous spindle cell tumors including fibromas, fibrosarcomas, neurofibromas, schwannomas, and hemangiopericytomas (13–16).

The prevalence and distribution of lesions in *S. flavidus* appear to reflect the relative number and distribution of chromatophores in normal skin. *S. flavidus* has a normal predominance of dermal melanophores (concentrated dorsally), followed in number by xanthophores (primarily in fins) and then erythrophores (located in small red-brown spots over the flanks). Accordingly, melanophore lesions were most common, followed by xanthophore lesions, and then erythrophore lesions (the least common). The dorsal and anterior distribution of melanophore hyperplasia and melanophoromas in *S. flavidus* is also probably a function of normal melanophore location.

Etiology is currently unknown. Potential etiologies include oncogenic viruses, genetic predisposition, normal aging phenomena, UV and ionizing radiation, and exposure to xenobiotic compounds. Although oncogenic retroviruses have been clearly implicated in mammalian lymphoma, leukemia, and sarcomas (17), there has been little evidence to support a viral etiology with respect to melanomas in mammals. The association between oncogenic viruses and neoplasia in fish is less common but has been established with lymphoma in northern pike (*Esox lucius*) (18–21), epithelial tumors in masou salmon (*Onchorhynchus masou*) (22–24), and dermal sarcomas in walleye (*Stizostedion vitreum*) (25–27). No viral particles were seen in any rockfish lesions, but the amount of tissue examined was limited, and a viral etiology cannot be definitively ruled out.

Genetic predisposition to melanoma is well documented in domestic animals (13) and humans (28, 29), and melanophoromas are readily induced in selective platyfish-swordtail hybrids (*Xiphophorus maculatus* crossed with *X. helleri*) (30–32). It is unlikely, however, that fish from Cordell Bank are a highly inbred, isolated group of fish. Rockfish have a pelagic larval stage and are probably randomly distributed by ocean currents following the fertilization of eggs. In addition, recent analysis of ribosomal genes from mitochondrial DNA revealed no significant differences between populations of *S. flavidus* from Cordell Bank, West Port in central Washington, and Vancouver Island, British Columbia.[6] The involvement of at least five different species would also appear to decrease the likelihood that genetics plays a critical etiological role.

Although both lesion prevalence and severity in *S. flavidus* increased with age, it is also unlikely that age is the only or predominant factor. Age-associated increases in pigment cell tumor prevalence have been documented in both goldfish (10) and *Xiphophorus* hybrids (33), and almost all species of mammals have higher prevalences of benign and malignant tumors with increasing age. The increased tumor prevalence in both fish and mammals, however, is usually more [illegible] uniform throughout a given population as it ages. If lesions were primarily age related, we would have expected to see rockfish with lesions throughout the Pacific coast. Instead, affected fish were concentrated at Cordell Bank. The higher prevalence in older *S. flavidus* may simply be a function of the slow progression of the disease following exposure and initiation at an early age.

One potential source of neoplastic initiation is exposure to UV radiation from sunlight. Although exposure to UV radiation alone will not induce melanoma in mice (34), and human melanoma is not correlated with exposed skin surfaces, there is an extensive body of research which indicates fairly conclusively that UV radiation is involved in melanoma formation (35). UV radiation has also been shown to induce melanophoromas in platyfish-swordtail hybrids, and these fish have been proposed as an animal model for human malignant melanoma (36). Wild fish species (including *X. maculatus* and *X. helleri*), however, have not been shown to be susceptible to UV radiation-induced neoplasia. Additionally, there is minimal penetration of UV radiation through water, and it would seem unlikely that deep-water species of rockfish are receiving any significant exposure.

Ionizing radiation is another potential etiological agent that must be considered because of the relatively close proximity (30 km) of Cordell Bank to the Farallon Islands Radioactive Waste Dump (Fig. 1). Approximately 14,500 Ci of radioactive wastes were disposed of from

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[6] K. McGauley, Humboldt State University, CA, personal communication.

1946 to 1970 at three sites in 90 (site A), 900 (site C), and 1800 (site B) m of water (37–40). Several studies have already been conducted at the FIRWD (41–43), and most have concluded that sediments and biota are significantly contaminated with $^{239+240}$Pu and $^{137}$Cs. Estimates of sediment levels range as high as 2,208 times background for $^{239+240}$Pu (42) and 134 times background for $^{137}$Cs (43). Estimates of $^{239+240}$Pu levels in fish (various species) were as high as 8500 times background for muscle and 5071 times background for liver (42).

Although there is little evidence that ionizing radiation induces melanoma in either humans or laboratory mammals (44), radiation is linked with a wide range of mammalian neoplasms, and long-term effects in fish are unknown. It is interesting to note that scales in rockfish are often ossified and that exposure to $^{239}$Pu, which is specifically recognized for its propensity to localize in bone and induce osteosarcomas in mammals (45), could result in localization in scales. Sequestration of $^{239}$Pu immediately adjacent to dermal chromatophores would certainly enhance the possibility for neoplastic transformation or promotion.

In addition to radioactive compounds, the FIRWD was also extensively used as a chemical waste disposal site, with approximately 47,800 drums of unspecified waste being dumped from 1946 to 1970 (46). Limited sampling has already revealed high levels of chlorinated hydrocarbons (dichlorodiphenyltrichloroethanes and polychlorinated biphenyls) in sablefish (*Anoplopoma fimbria*) and dover sole (*Microstomus pacificus*) (47). While dichlorodiphenyltrichloroethanes and polychlorinated biphenyls have not been directly linked with melanoma in mammals, both are considered hepatic carcinogens in laboratory animals (48, 49), and there is at least one report of a slightly increased incidence of melanoma in a group of men occupationally exposed to polychlorinated biphenyls (50, 51).

Polyaromatic hydrocarbons have been definitively linked with melanoma in mammals, and 7,12-dimethylbenz[*a*]anthracene is capable of inducing melanoma via direct skin painting in hamsters, guinea pigs, and mice (35). Interestingly, Japanese researchers studying epizootics of chromatophoromas in *N. mitsukurii* were able to induce both chromatophore hyperplasia and neoplasia in laboratory-reared *N. mitsukuri* using several known carcinogens including 7,12-dimethylbenz[*a*]anthracene (7). Japanese researchers were also able to induce melanophore hyperplasia in 70–100% of marine catfish (*Plotosus anguillaris*) and chromatophoroma in one *N. mitsukurii* using effluent from a kraft pulp mill epidemiologically linked with identical lesions in wild fish (52). The Japanese study is one of the few examples where the hypothesis that chromatophoromas in wild fish are caused by exposure to carcinogenic compounds has been tested, at least partially, under controlled laboratory conditions.

There are a number of ways that fish from Cordell Bank may be exposed to radioactive or chemical compounds from the FIRWD. While the dominant surface current off California (the California current) runs north to south, surface waters near the Farallons are controlled from October through March by the northward-flowing Davidson counter-current (38). Deep bottom currents at the FIRWD are more complex, but Crabbs (53) did find a predominantly northward-flowing current from site B. There may also be some northward migration of rockfish in response to El Niño (warm water current), and adult Cordell rockfish may have been exposed as larvae or juveniles at the Farallons prior to being carried north.

Efforts are under way to expand the study area to include the FIRWD, but much additional work needs to be done in order to establish a more definitive link between the cutaneous lesions in rockfish and possible exposure to carcinogenic compounds in the environment.

## ACKNOWLEDGMENTS

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# Subsurface Fish Handling to Limit Decompression Effects on Deepwater Species

FRANK A. PARRISH and ROBERT B. MOFFITT

## Introduction

Fish commonly suffer barotrauma caused by rapid decompression as they are hauled to the surface by conventional fishing techniques. The problems are more serious for fish caught at greater depths and especially for physoclistous fishes with closed swim bladders. Common physical effects of such drastic volume changes are everted stomachs, eyes forced from orbits, and distortion of scales and subcutaneous flesh.

Barotrauma can have implications for the success of some research investigations. Regurgitation and stomach eversion adversely affect research results in dietary studies (Bowman, 1986). Fish in tag-and-recovery studies suffer increased mortality and their natural behavior may be altered (Grimes et al., 1983; Matthews and Reavis, 1990). Hauling snappers to the surface at slow or controlled rates does not greatly reduce the effects of barotrauma (Haight, 1989). Attempts to relieve distended air bladders at the surface by puncture using hypodermic syringe needles 1) require repositioning of fish stomachs, 2) involve more handling, and 3) do not eliminate the risk of internal injury during hauling. An injured bladder may not be capable of regulating volume properly, or at best it may require a prolonged recovery period (Harden-Jones, 1957). Thus, fish returned to native depths with artificially vented gas bladders may have trouble maintaining normal buoyancy and behave abnormally for an unknown period of time after release.

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*ABSTRACT—A method of handling hooked fish at intermediate depth was developed for species which occur deeper than conventional scuba depths. Juvenile pink snappers,* Pristipomoides filamentosus, *were hauled from 65–100 m to a depth of only 30 m, where the ambient pressure change was a fraction of that produced by hauling fish to the sea surface. This method afforded a unique opportunity to acoustically tag deepwater, physoclistous fish without the need to alter the fish's original swim bladder volume and without the high risk of further injury associated with surface handling. Tagged* P. filamentosus *survived and behaved well and were tracked successfully. This basic method could be applied to a variety of deepwater species in a number of research approaches, including tagging and dietary studies.*

Studies (Matthews and Reavis, 1990; DeMartini et al.[1]) have shown that fish tagged at depth by scuba divers provide a greater number of tag returns than those tagged at the surface by conventional techniques. Methods for successful tagging at depths inaccessible to scuba divers have been developed by Grimes et al. (1983) using breakaway hooks and by Priede and Smith (1986) using an ingestible acoustic tag. Unfortunately, neither method provides information as to the size (or even species in the case of Grimes et al. (1983)) of the tagged individual at the time of tagging, and both methods are poorly suited to multispecies fishery situations.

In the course of studying the juvenile Hawaiian snapper, *Pristipomoides filamentosus*, we have found it necessary to tag individuals acoustically to evaluate their diel movement patterns. However, these fish routinely suffer severe barotrauma when hauled to the surface from their normal depths of 65–100 m (Parrish, 1989). Assuming unrestricted expansion, a fish brought from 65 m may experience a 7.5-fold increase in gas volume in its swim bladder. Surface handling of the fish for release, including venting the swim bladder with a syringe and repositioning the stomach when everted, has resulted in only about 40–50% survival at the surface and an unknown additional mortality after release (Moffitt and Parrish[2]). The small size of the fish, 8–25 cm fork length (FL), adds a further complication by restricting acceptable transmitter size, which in turn limits its battery life. A short battery life requires that collection of data representative of normal fish behavior begin at once and not be affected by buoyancy problems associated with an artificially vented swim bladder.

To prevent these problems with our acoustically tagged fish, we developed a subsurface handling method which is also applicable to other tagging and dietary study programs. The interception of hauled fish at an intermediate depth by divers offers the potential to prevent damaging barotrauma by minimizing expansion of the swim bladder.

## Methods

### Transmitter Placement

Because of the small size of our fish, we used the smallest available transmitter (approximately 8 mm diameter × 35 mm long) and restricted the size of our target fish to ≥15 cm FL. The transmitter was introduced orally and pushed down the esophagus of the fish by a small dowel (8 mm diameter × 18 cm long), equipped with a sleeve to hold the transmitter. Small barbs attached to the transmitter assisted in lodging and retaining it in the gut of the fish (Fig. 1). The time required to implant the transmitter never exceeded 5 seconds. The effects of tagging and tag retention were also evaluated in a tank experiment in which dummy transmitters were implanted in two juvenile snappers as described above and observed over a 3-week period.

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[1] DeMartini, E. E., A. M. Barnett, T. D. Johnson, and R. F. Ambrose. In review. Growth and production estimates for biomass-dominant fishes on a southern Californian artificial reef. Bull. Mar. Sci.

[2] Moffitt, R. B., and F. A. Parrish. Unpublished data on file at Honolulu Lab., Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

### Subsurface Tagging Operations

The "tagging array" (Fig. 2) consisted of a polypropylene line connected to a rectangular wire trap (100 × 75 cm) which was suspended 30 m below a surface buoy loosely roped to a surface support vessel. Shock absorbing cords were affixed to the line at both the buoy and trap ends to minimize the effect of surface movement on the trap. Attached to the line 17 m below the surface was a T-bar where divers waited to intercept fishing lines hauled by fishermen in the boat.

When a fish was hooked, a fisherman reeled the monofilament line in until a premeasured depth mark on the line was reached. A carabiner was clipped around both the fishing line and a taut high-test monofilament "transport line" connected between the fishing boat and one end of the T-bar. The heavy carabiner slid down the transport line, pulling the fishing line close to the array and the waiting divers. The divers were then able to find the nearly invisible monofilament fishing line at the end of the T-bar and proceed with the tagging operations.

If the divers determined that the fish on the line was not suitable for tagging, a diver signaled the surface crew to continue fishing by clipping a particular color-coded buoy around the fishing line and freeing it from the T-bar. Once a suitable fish was hooked, they descended to the 30 m depth where the hooked fish hung suspended close to the wire holding trap. Wearing latex gloves to protect the fish, a

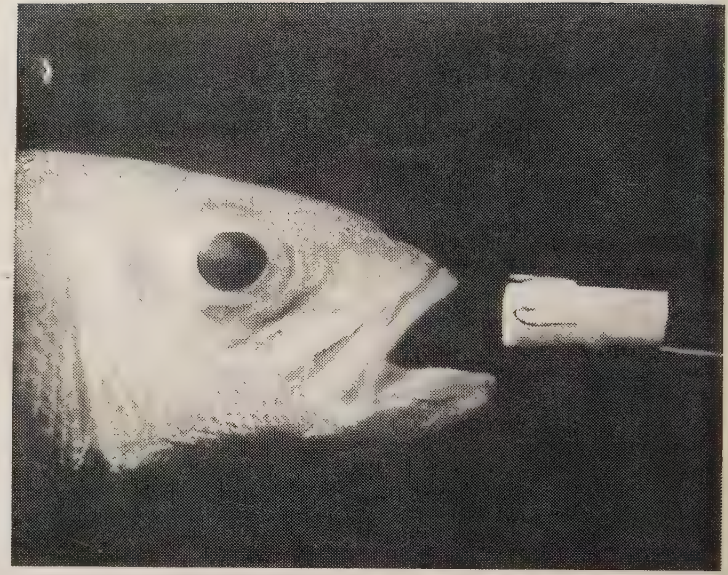

Figure 1.—An intragastric acoustic transmitter (35 mm long) being implanted in a juvenile pink snapper.

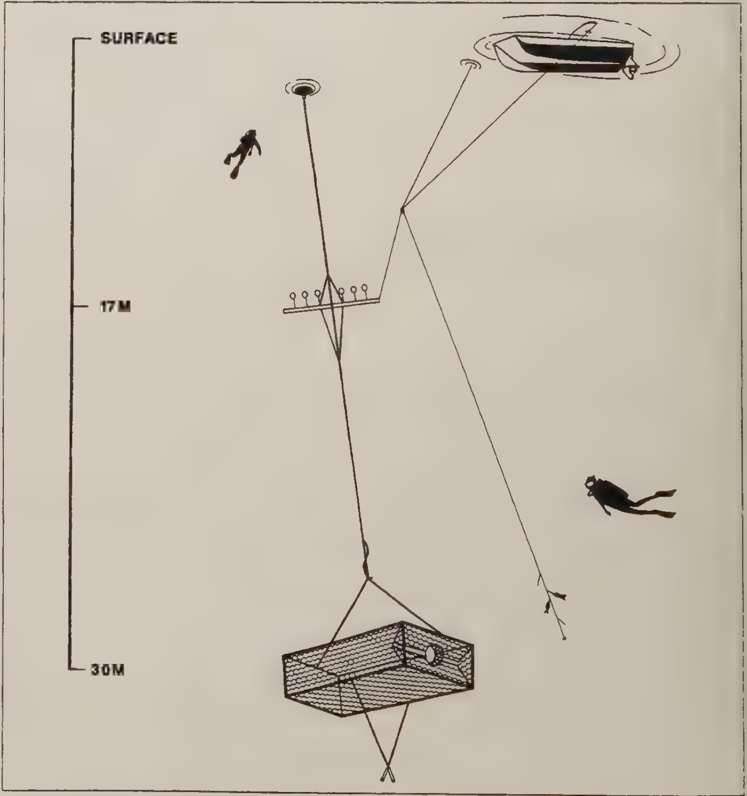

Figure 2.—Schematic representation of the subsurface tagging array.

diver restrained the fish while using the modified dowel to push the transmitter down its gullet. The fish was then removed from the hook, and its FL measured with a scale (mounted on the trap) as the fish was placed in the trap through an escape-proof entrance. The trap was lined with fine mesh synthetic netting to cushion the interior. Fishermen in the boat were signaled to stop fishing by clipping a different color-coded buoy to the empty fishing line and releasing it from the T-bar. Each tagged fish was held in the trap for about 5 minutes, allowing evaluation of its physical condition before release with the transmitter installed. If the appearance or behavior of the fish seemed questionable, the diver dissected the fish and recovered the transmitter for implantation in the next suitable fish. If the tagged fish demonstrated brisk activity and normal orientation in the trap, it was released by a hinged panel being opened on the trap (Fig. 3).

## Results and Discussion

Using the methods described above, we successfully implanted tags in juvenile snappers on each of five trials. None of the 17 fish that were brought to 30 m from depths of 65–90 m had everted stomachs or other obvious symptoms of barotrauma. This is not unexpected because, assuming unrestricted gas expansion, a fish brought from 65 m to 30 m would experience 1.9-fold expansion of its swim bladder instead of a possible 7.5-fold expansion if it were brought to the surface. Ten fish were not selected for tagging: Some were too small (<15 cm FL), and others were hooked deep in the mouth and therefore risked damage to gills or esophagus when the hook was removed. Two of the seven fish tagged had poor color and experienced difficulty orienting while in the holding trap. They were sacrificed to recover the transmitters. The remaining five fish were successfully tagged and released. Released fish swam immediately toward the bottom.

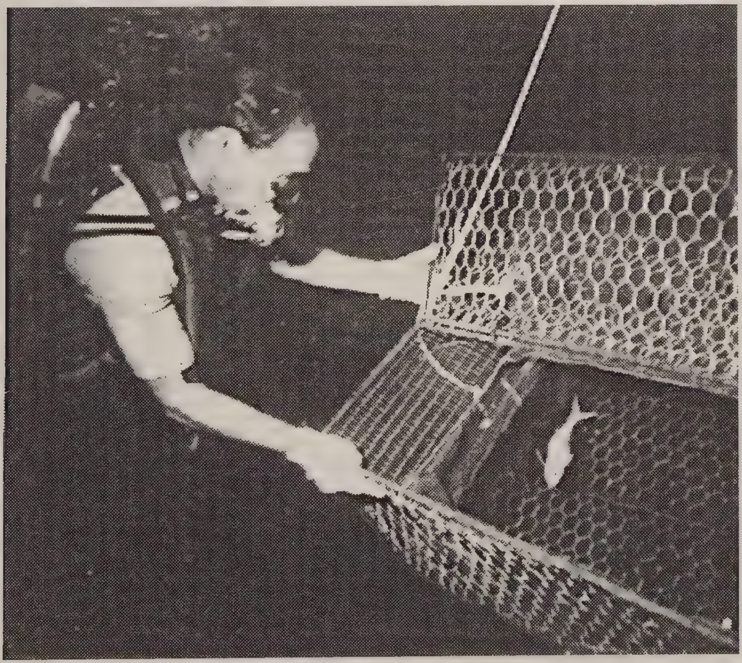

Figure 3.—Release of a juvenile pink snapper implanted with an acoustic transmitter at 30 m depth.

One of the two fish implanted with dummy transmitters in the holding tank died immediately. Death was probably due to internal injuries sustained when the transmitter was inserted. The second tagged fish in the tank study fed and behaved normally with the five conspecifics with which it was held throughout the 3-week period.

We elected to implant transmitters orally because of the ease of application by divers and the minimal handling time required. We anticipated success since others (McCleave and Stred, 1975; Hawkins and Urquart, 1983; Mellas and Haynes, 1985; Lucas and Johnstone, 1990) have reported minimally altered behavior of fish with gastric transmitter implants. Our resulting tracks, using this technique in our subsurface tagging, provided data with consistent behavioral trends over the 5-day duration of each track.

Our subsurface handling method has potential application to dietary and tag-release studies for a number of deepwater species. The need for such a technique and its effectiveness will probably vary with the depth of capture and the physiological tolerances of individual species. In dietary studies, fish could be removed from the hook and bagged at depth prior to regurgitation and stomach eversion, thus ensuring the integrity of the food sample. In tagging studies, including acoustic tracking, advantages include minimum handling (all in the water), reduced trauma from excessive swim bladder distension, avoidance of the effects of surgical puncture of the bladder, and opportunity to observe the condition of the fish before release. All these features increase the likelihood of releasing healthy, normal fish. However, the method is labor intensive (requiring a minimum of three people), and fishing time is limited by the time at depth safe for the divers. Therefore, the method may only be effective in situations where the target species can be caught readily.

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# Biology of the Pacific Pomfret (*Brama japonica*) in the North Pacific Ocean

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Abundances of Pacific pomfret (*Brama japonica*), an epipelagic fish of the North Pacific Ocean, were estimated from gillnet catches during the summers of 1978–1989. Two size modes were common: small pomfret <1 yr old, and large fish ages 1–6. Large and small fish moved northward as temperatures increased, but large fish migrated farther north, often into the cool, low-salinity waters of the Central Subarctic Pacific. Lengths of small fish were positively correlated with latitude and negatively correlated with summer surface temperature. Interannual variations in the latitude of catches correlated with surface temperatures. Large catches were made in the eastern Gulf of Alaska (51–55°N) but modes of small pomfret were absent here, and large fish were rare at these latitudes farther to the west. Pomfret grow rapidly during their first two years of life. They are pectoral fin swimmers that swim continuously. They prey largely on gonatid squids in the region of the Subarctic Current in the Gulf of Alaska during summer. No evidence was found for aggregations on a scale ≤1km. Differences in the incidence of tapeworm, spawning seasons, and size distributions suggest the possibility of discrete populations in the North Pacific Ocean.

L'abondance de la casthagnole mince (*Brama japonica*), un poisson épipélagique du Pacifique nord, a été estimée à partir des prises par filets maillants des étés 1978 à 1989. Deux classes de taille étaient communément trouvées : la petite casthagnole de moins de 1 an et la grande de 1 à 6 ans. Les uns comme les autres migrent vers le nord à mesure que la température s'élève, mais les plus gros se rendent plus loin au nord, souvent dans les eaux fraîches et peu salines de la partie centrale du Pacifique subarctique. Il existe une corrélation positive avec la latitude et une corrélation négative avec la température de l'eau de surface en été, et la longueur des petits poissons. Les variations d'une année à l'autre de la latitude des prises sont en corrélation avec la température de surface. Les grosses prises ont été faites dans la partie est du Golfe d'Alaska (51–55°N), mais les petits casthagnoles ne sont pas trouvés dans ce secteur, et les gros sont rares à la même latitude, mais plus à l'ouest. La casthagnole grossit rapidement durant ses deux premières années. Ce poisson se propulse avec ses nageoires pectorales et nage continuellement. Il se nourrit abondamment l'été des calmars gonatidés dans le Golfe d'Alaska ou dans la région où passe le courant subarctique. Rien n'indique qu'il y ait des agrégations de cette espèce sur une échelle égale ou inférieure à 1 km. Les différences dans le taux d'infestation par le ténia soulèvent la possibilité qu'il existe des populations distinctes dans le Pacifique nord.

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The Pacific pomfret, *Brama japonica* Hilgendorf (family Bramidae), is an abundant and widely distributed epipelagic fish in the North Pacific Ocean. It migrates from subtropical waters into feeding grounds north of the Subarctic Boundary during late spring and summer periods of high productivity (Neave and Hanavan 1960; Sasaki et al. 1981; Wada and Murata 1985; Brodeur 1988; Shimazaki 1989). During fall and winter, pomfret migrate rapidly into waters south of the Subarctic Boundary (Shimazaki and Nakamura 1981) where spawning occurs during winter through early spring near the Subtropical Frontal Zone in the western Pacific (Yoon and Shimazaki 1981; Shimazaki and Nakamura 1981).

The abundance of pomfret in the North Pacific is documented by their huge bycatch in the Japanese, Taiwanese, and Korean drift gillnet fisheries for flying squid (*Ommastrephes bartrami*). The estimated total number of Pacific pomfret caught by vessels of these nations was 1329 million and 82 million in 1990 and 1991, respectively (DiNardo and Kwok, unpublished data). In some years, the catch of pomfret was about one-half that of flying squid (Yatsu et al. 1993). Moreover, these bycatches may be underestimates because pomfret drop out of the gill nets during retrieval and accurate counts are not possible when large numbers are caught (Int. North Pac. Fish. Comm. 1991). LeBrasseur et al. (1987) estimated that 100–300 million pomfret may have been discarded annually in the Japanese fishery alone. Drift gill nets fished for flying squid off British Columbia also caught large numbers of pomfret; sometimes it was the most abundant species (Robinson and Jamieson 1984; Jamieson and Heritage 1987).

Pacific pomfret is greatly underutilized as a food fish. Some are landed in countries bordering the western Pacific, and a few are marketed in United States. It has excellent flavor to the palate

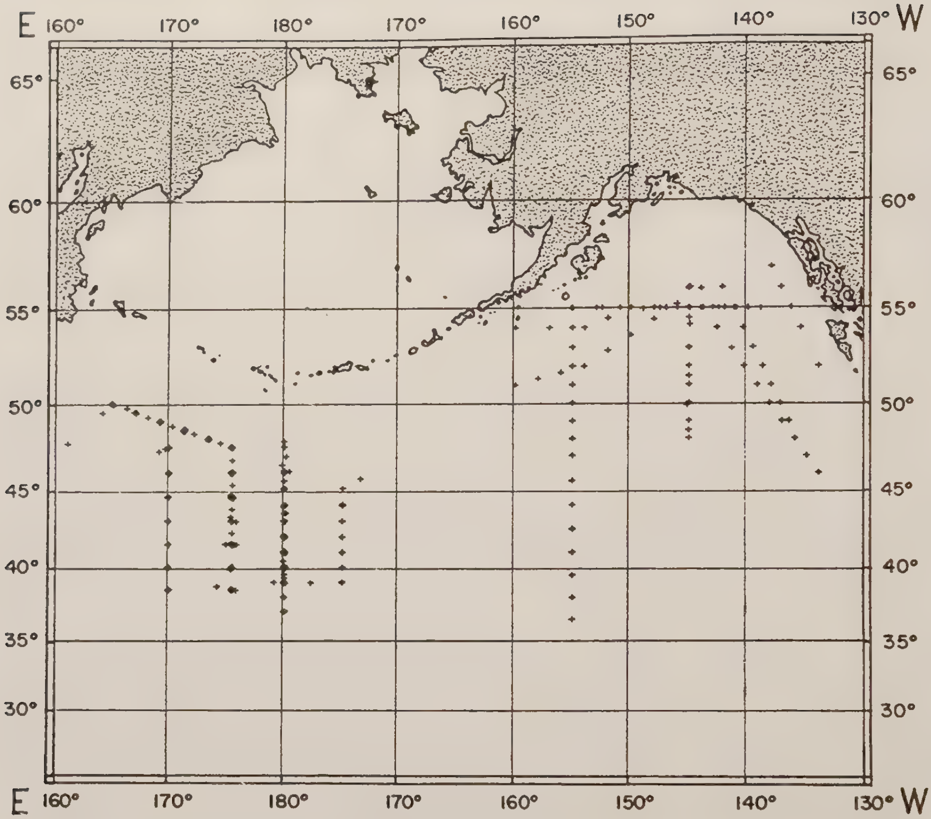

FIG. 1. Location of gillnet stations, 1978–89, by training ships from Hokkaido University. The transects along 180°, 175°E, and 170°E were repeated during most years (see text).

of North Americans (Elwell 1987).

Because of the abundance of Pacific pomfret, its important ecological role in these oceanic regions, and its potential for sustaining a large commercial fishery, better understanding of the biology and ecology of this species is needed (Shimazaki 1989). Based on results of 12 yr of gillnet cruises by Hokkaido University, we present information on geographic variations in size distributions, interannual trends in abundance relative to ocean conditions, patchiness of catches in gill nets, age and growth, food habits and parasites, and observations on swimming behavior of Pacific pomfret.

## Methods

Data on catches of Pacific pomfret in gill nets together with oceanographic data were collected during summer cruises from 1978 to 1989, by the Hokkaido University Training Ships (T/S) Oshoro Maru along 180° and in the Gulf of Alaska (130°–165°W) and Hokusei Maru between 165°E and 180° (Fig. 1). Gill nets, 4550–6600 m long and 6.7 m deep, were fished overnight. Gill nets fished from the Oshoro Maru usually included 150–250 m (3–5 tans, one tan = 50 m) each of 29, 33, 37, 42, 48, 55, 63, 72, 82, 93, 106, 138, 157, 179, and 204 mm (stretched) mesh, 1000–1400 m (20–28 tans) each of 115 and 121 mm mesh, and 500–1000 m (10–20 tans) of 130 mm mesh. Gill nets fished from the Hokusei Maru usually included 50–150 m (1–3 tans) of 19, 22, 25, 29, 33, 42, 48, 55, 63, 72, 82, 93, 106, 138, 157, 179, 204, and 233 mm mesh, and 500–1000 m (10–20 tans) of 112, 115, 118, and 121 mm mesh (see Hokkaido University 1979–90 for details on gill nets, catches and oceanographic observations). Of the 385 sets that were completed during these years, 253 caught 92 439 pomfret. A total of 20 799 was measured to the nearest millimeter fork length (FL), including samples from each mesh size.

Temperature and salinity were measured at each gillnet station, and usually midway between gillnet stations, from the surface to a depth of at least 700 m. Dynamic height anomalies relative to 700 dbar were calculated by integrating specific volume anomalies (Fofonoff and Millard 1983) over pressure.

### Estimating Abundance of Pacific Pomfret

A gill net fishing equal numbers of tans in a geometric size series of meshes, with each mesh approximately 14% larger than the preceeding one, is non-size-selective for Pacific pomfret from 160 to 520 mm FL (Shimazaki et al. 1981). The non-selective gill net described by Shimazaki et al. (1981) consisted

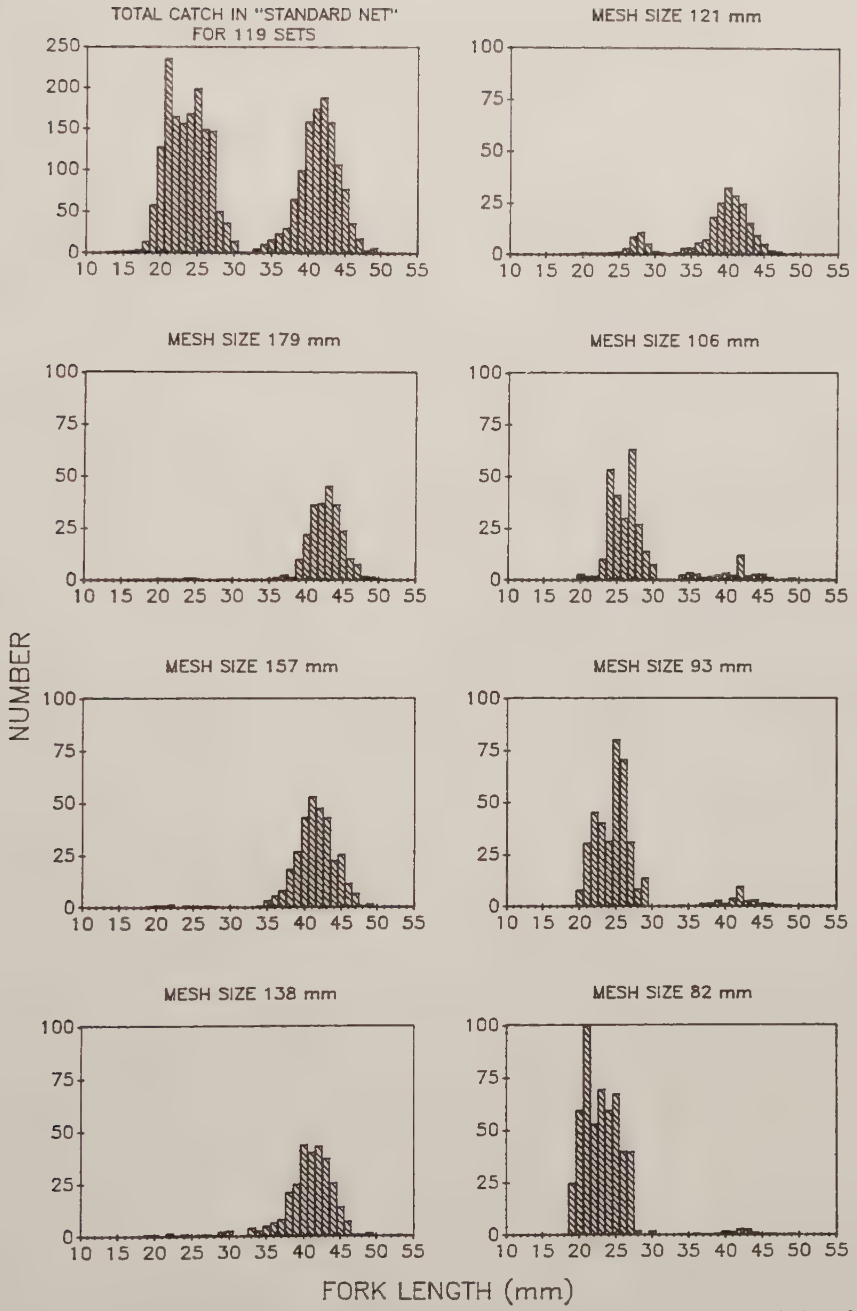

FIG. 2. Length–frequency distributions of pomfret caught in 119 sets of the "standard net" for the mesh sizes of Shimazaki et al's. (1981) non-selective gill net (excluding the 204 and 233 mm meshes). (*Fig. 2 concluded next page*)

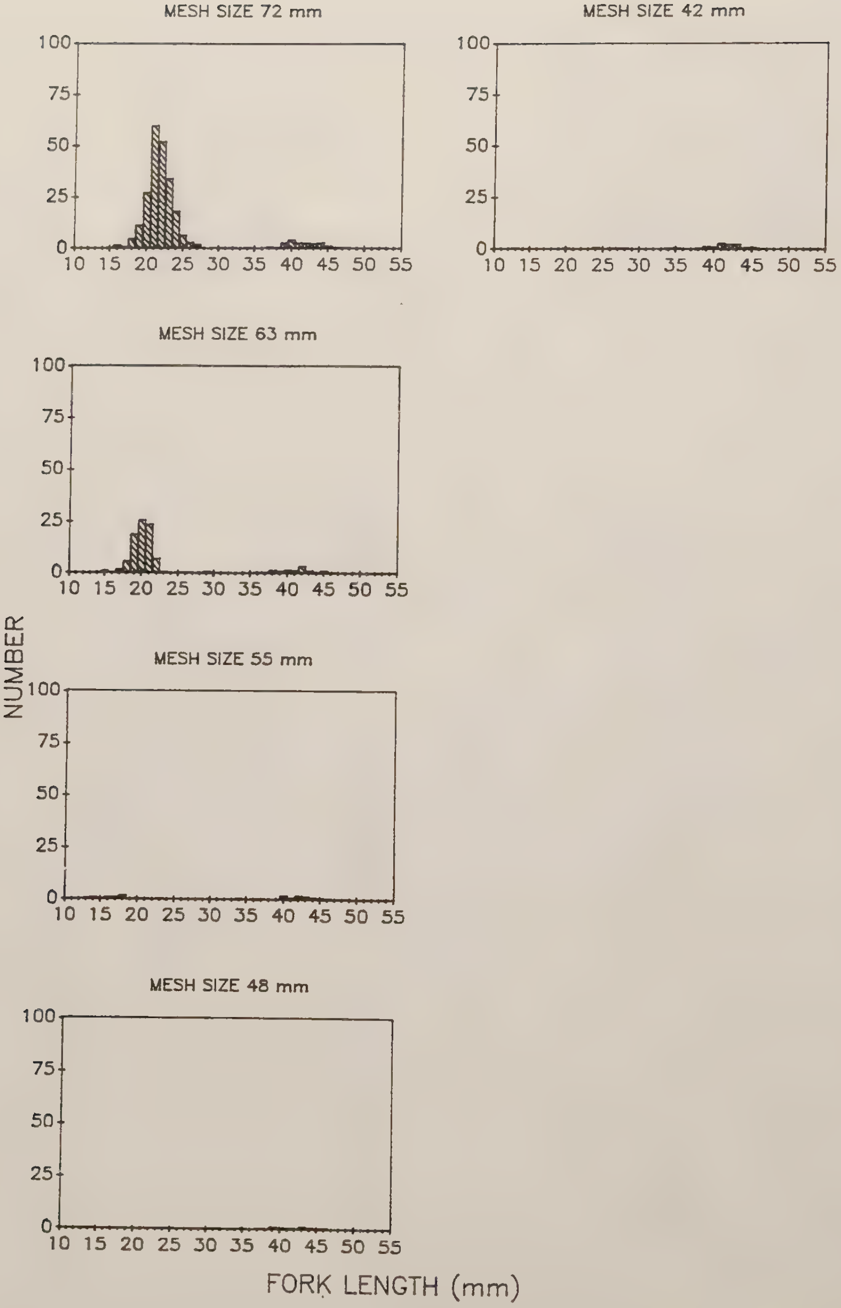

FIG. 2. (*Concluded*)

of 42, 48, 55, 63, 72, 82, 93, 106, 121, 138, 157, 179, 204, and 233 mm meshes. Standardized catches for each mesh size of this geometric series through 179 mm mesh (Fig. 2) show that small meshes (<106 mm) caught predominantly small (≤330 mm FL) pomfret and large meshes (121–179 mm) caught mainly large (>330 mm FL) pomfret. In our study, gill nets departed from the "research net" described by Shimazaki et al. (1981) chiefly in that many tans of 112, 115, 118, 121, and 130 mm mesh were

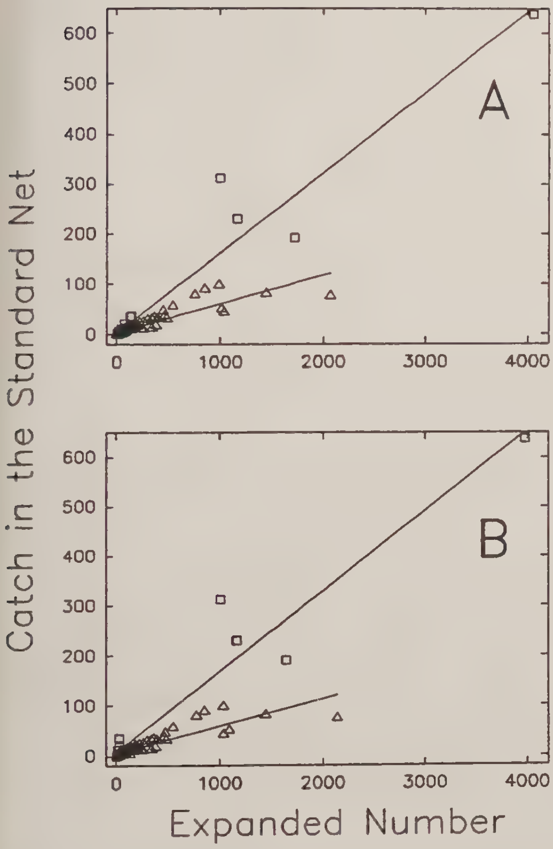

FIG. 3. (A) Regressions of catch of large and small pomfret in the standard net on the numbers of measured small and large pomfret expanded to equal the total catch in the set. Data are from 157 sets for which catch in the standard net could be determined directly (Method 1 in text). These regressions were used to estimate catch in the standard net in 69 sets where data were inadequate to determine catch directly, but where fish were measured from most mesh sizes (Method 2 in text). Small fish (squares), $n = 78$, $Y = 0.16X + 1.47$, $r = 0.97$. Large fish (triangles), $n = 137$, $Y = 0.06X + 3.41$, $r = 0.89$; (B) Same as 3(A), but expansions were based on the numbers of large and small fish in the 121 mm mesh only. Regression between catch in the standard net and the expanded numbers of small and large pomfret from 121 mm mesh were used to estimate catch in 22 sets where only fish from the 121 mm mesh were measured (Method 3 in text). Small fish (squares), $n = 29$, $Y = 0.16X + 5.69$, $r = 0.97$. Large fish (triangles), $n = 121$, $Y = 0.05X + 3.9$, $r = 0.88$.

fished in addition to the standard geometric series. Often these non-standard meshes accounted for over 50% of all tans in the gill net. In addition, small meshes between 19 and 37 mm were fished. Gillnet configurations consisted of as few as 12 and as many as 23 different sizes of mesh, and the total numbers of tans fished ranged from 63 to 133.

Because of the variability in net configuration, and the consequent variability in selectivity for different sizes of pomfret, raw catches in the different gill net sets were poor estimates of size-specific abundances of pomfret. To estimate relative abundance of small (≤330 mm FL) and large (>330 mm FL) pomfret caught in different sets and cruises, we converted raw catch in each gill net set to an estimated catch in the standard net described by Shimazaki et al. (1981). Depending on the completeness of catch data, one of three methods was used to make this conversion:

*Method 1*

Complete mesh-by-mesh catch data for pomfret were available for 157 sets. Total catches and size-frequency distributions of fish from subsamples were known for each mesh size in these gillnet sets. Total numbers of small and large fish caught in each mesh size were estimated by expanding the numbers in the measured subsample for each mesh. Catch data for each mesh were converted to catch/tan by dividing by the number of tans fished of the corresponding mesh. Catches/tan in each mesh in the geometric series described by Shimazaki et al. (1981), with the exception of the 204 and 233 mm meshes that were often missing, were added to give catch of large and small fish in a standard non-selective net in which one tan of each standard mesh was fished. This standardized catch, called "catch in the standard net," was the basis for our comparisons of abundance.

*Method 2*

In 69 gillnet sets, total catch of pomfret in the gill net and the size-frequency distributions of subsamples from the different meshes were known, but catch in each mesh was not known. Therefore, no estimate could be made of total catch of large and small fish in each mesh. Because catch in the standard net could not be calculated directly, it was estimated in two steps. The ratio of large and small fish in the measured sample from all meshes combined was expanded to the entire catch:

$$\text{No. small (large) fish} = \frac{\text{measured small (large) fish}}{\text{all measured fish}} \times \text{total catch.}$$

The expanded numbers of large and small fish were converted to catches in the standard net using regressions of these two abundance estimates for large and small fish from the 157 gillnet sets where catch in the standard net could be calculated directly (Method 1) (Fig. 3A). Because of the many extra meshes in the size range from 112 to 130 mm, the abundance of large fish relative to small fish in the measured sample was usually greater than that in the standard net. High selectivity of the gill nets for large fish and low selectivity for small fish are indicated by the lower slope of the regression for large fish than for small fish (Fig. 3A).

*Method 3*

In 22 sets, fish were measured in the 121-mm mesh and, at most, in one additional mesh. Catches in the standard net were converted from numbers of large and small fish in the 121-mm mesh expanded to equal the total catch in the set using regressions for large and small fish from the 157 complete sets, as in Method 2. The regressions are similar to those of Method 2 (Fig. 3B), indicating that the 121-mm mesh and the non-standard gill net caught similar ratios of large and small fish (see Fig. 2). In five sets, pomfret were caught, but none was measured and abundance was not estimated.

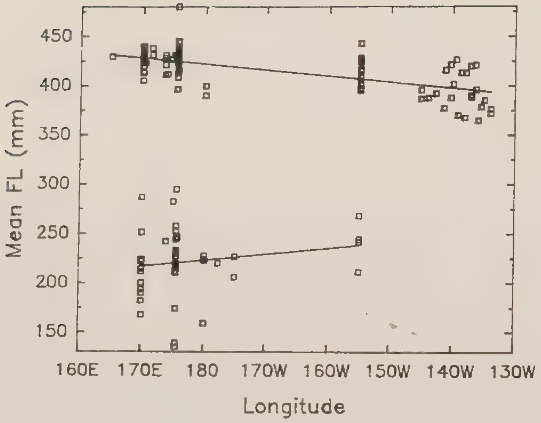

FIG. 4. Mean fork lengths of the distinct modes of small and large pomfret caught in the standard net during July vs. longitude of capture based on 157 sets with complete catch by mesh data.

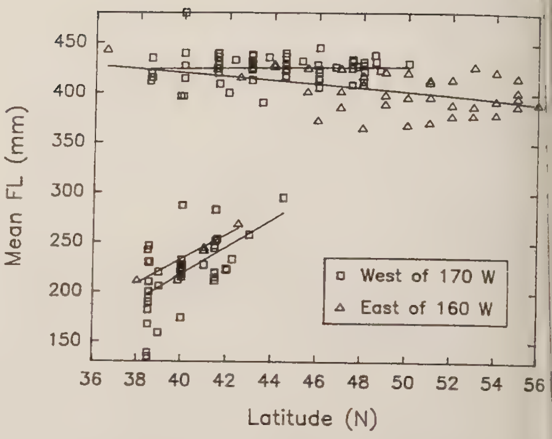

FIG. 5. Mean fork lengths of the distinct modes of small and large pomfret during July vs. latitude (squares, west of 170°W; triangles, east of 160°W) based on 157 sets with complete catch by mesh data.

### Aggregation of Catches

The patchiness in abundance of pomfret caught within gill nets was examined from numbers of fish caught in contiguous tans of the same mesh size. In 26 instances, 10–20 tans of either 115, 121, or 130 mm mesh were fished in a continuous series. Coefficients of dispersion (variance/mean ratios) of the catch per tan were tested against a random distribution, assuming that they were distributed as a chi-square variate.

### Age and Growth

Sagittal otoliths were removed from Pacific pomfret collected in the eastern North Pacific (135°–155°W) onboard the Oshoro Maru during the summers of 1985 and 1987, and stored dry (1985) or in a 50% glycerin-water solution with thymol added as a preservative (1987). A few small, whole pomfret were frozen in 1985 and otoliths were removed and fish lengths and sex recorded in the laboratory. All otoliths were cleaned in the laboratory and stored in 80% ethanol.

Otoliths were submerged in water on a black background, and distal surfaces were examined at 32–80× magnification under a Wild M3 dissecting microscope with reflected light. A white or opaque band, representing rapid growth, and an adjacent narrower dark or translucent band, deposited during periods of slow growth, were interpreted as 1 yr of growth, although increment periodicity remains unvalidated for this epipelagic species. The type of growth on the edge of the otolith was noted. Transverse and longitudinal sections were taken from many otoliths.

Narrow, fine-scale bands, presumed to represent daily growth increments, were counted on sagittal sections of otoliths from the smallest pomfret following the methodology of Boehlert and Yoklavich (1985). Increments were counted at 1000× magnification using a compound microscope and transmitted light. Increments appeared as distinct, concentric rings around the focus but became progressively smaller and less distinct toward the edge of the otolith.

### Food Habits

Major prey taxa were determined from examination of stomach contents of 979 Pacific pomfret caught east of 180°. In 1980, stomachs were removed, frozen at sea, and preserved in 10% formalin ashore. Food items were identified and major prey taxa were weighed. In 1981, frequency of occurrence of major prey was calculated. In 1984, 1985, 1986, and 1987, percent composition of major prey taxa was estimated visually at sea. In all years, common prey taxa were preserved and identified. Indices of stomach fullness were estimated as 0 (empty), 1 (to $\frac{1}{4}$ full), 2 ($\frac{1}{4}$ to $\frac{1}{2}$ full), 3 ($\frac{1}{2}$ to $\frac{3}{4}$ full), and 4 (full, rugae of stomach not apparent, stomach lining thin). State of digestion of stomach contents was also noted as fresh (1), partially digested (2), and well-digested (3).

### Parasites

Pacific pomfret from stations east and west of 180° were examined for larval tapeworms imbedded in the flesh. In all, 53 fish were frozen and examined in the laboratory ashore. Each fish was filleted and each of the four fillets from a fish, with skin removed, was candled with a lamp to detect tapeworms. When possible, the entire parasite was removed for identification.

### Swimming Behavior

In 1987, pomfret caught on hook-and-line from a depth of about 20–30 m during the daytime were immediately placed in a 90 × 122 × 75 cm deep tank with circulating sea water on board the Oshoro Maru. Swimming behavior and gill ventilation were observed over 24 h.

## Results and Discussion

### I. Geographic Variations in Size Distribution

The size distribution of the catches was almost always unimodal or bimodal with clearly separated modes (see also Machidori and Nakamura 1971; Wada and Murata 1985; Shimazaki 1989), enabling classification of fish into two size groups: small fish (130–330 mm) and large fish (331–500 mm) (Fig. 2). Few fish of intermediate size were captured. Only 26 of over 20 000 pomfret measured were over 500 mm FL, and only three were over 600 mm FL. The largest was 614 mm FL.

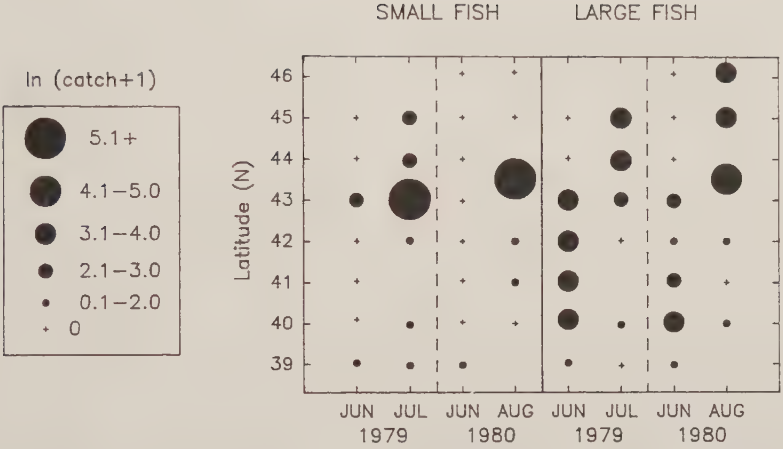

FIG. 6. Catches of small (≤330 mm FL) and large (>330 mm FL) pomfret in the standard net during early and late transects along 180°.

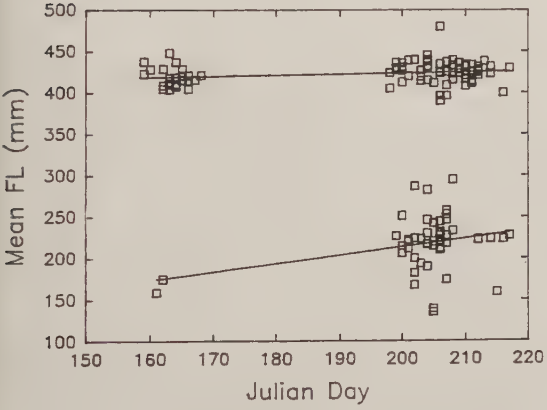

FIG. 7. Mean fork lengths of the distinct modes of small and large pomfret in the standard net vs. Julian date of capture for sets west of 170°W based on 117 sets with complete catch by mesh data.

The frequency of bimodal catches and the mean length of pomfret varied by location of capture. During July, when most sets were made, catches of small fish and bimodal catches of small and large fish were common in the western North Pacific (west of 170°W), whereas only four sets included modes of small pomfret in the Gulf of Alaska (Fig. 4). The mean lengths of the modes of large pomfret, but not small pomfret, decreased from the western Pacific to the Gulf of Alaska during July ($r = -0.65$, $P < 0.01$, $n = 81$, Fig. 4).

The size of pomfret in the standard net also varied with latitude. Modes of both small and large fish were common south of 44°N during July, but only large fish were caught north of 44°N. (Fig. 5). The largest percentage of sets with only modes of small pomfret occurred in southern waters, between 39° and 40°N. In addition, the mean FL of small fish was positively correlated with latitude ($P < 0.01$) both east of 160°W and west of 170°W, indicating that the smallest pomfret inhabited more southerly waters during the summer and did not migrate in high numbers into waters north of 44°N in this region. This trend was not found for large pomfret during July. Mean size of large pomfret decreased ($P < 0.05$) with latitude east of 160°W, but no

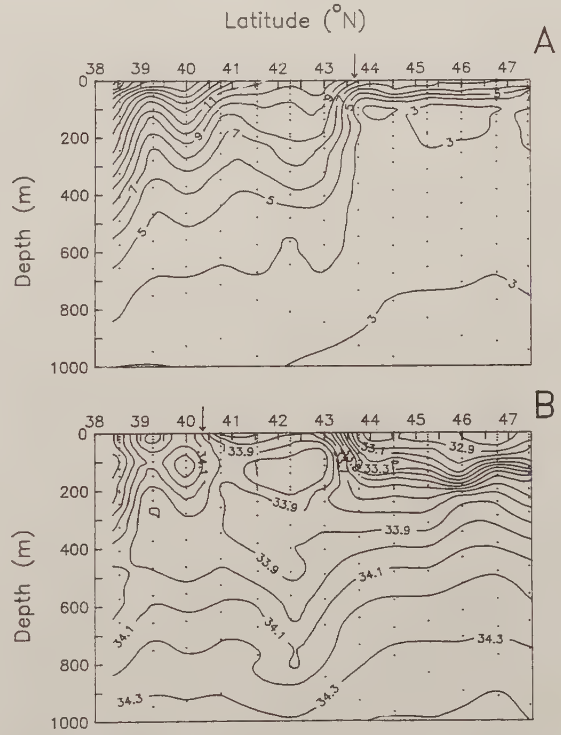

FIG. 8. Vertical section of (A) temperature and (B) salinity along 170°E during July 1983. The Subarctic Boundary is indicated by the intersection of the 34 ‰ isohaline with the surface, and the boundary between the Transitional and the Central Subarctic Domains of subarctic water is shown by the rapid descent of the 4°C isotherm below 100 m.

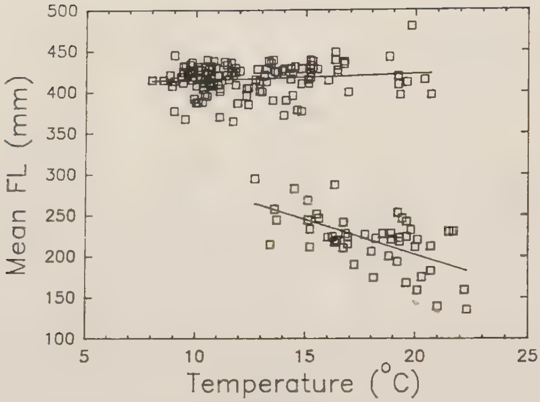

FIG. 9. Mean fork lengths of the distinct modes of small and large pomfret in the standard net vs. sea surface temperature based on 157 sets with complete catch by mesh data.

significant trend with latitude was found for large pomfret west of 170°W.

Mean length of pomfret increases from south to north during the summer in subarctic waters (Sasaki et al. 1981). Shimazaki (1989) reported that during the winter pomfret were only caught south of the Subarctic Boundary, whereas in early summer small pomfret (< 310 mm FL) were distributed south of the Subarctic Boundary (38°30′ to 43°N) while large pomfret were found in waters north of the boundary (45°30′ to 47°30′N, along 175°30′E). These trends indicate the more northerly migration of large fish during the summer.

North-south transects along 180°, conducted during June, July, or August, 1979 and 1980, clearly illustrate the northward movements of both small and large pomfret (Fig. 6). During these years, small pomfret (all fish ≤330 mm FL even if not in a distinct mode) were caught 2° farther to the north in July than in June 1979, and 4.5° farther to the north in August than in June 1980. These changes corresponded to movements northward of 2.7 and 5.1 miles per day, respectively. Large pomfret moved north by 2° in 1979 and 3.1° in 1980, corresponding to 2.7 and 3.8 miles per day, respectively.

Mean size of both small and large pomfret increased with date of capture ($P = 0.05$ and 0.07 respectively), although only two samples of small fish were measured in June (Fig. 7). The increase in size of small and large pomfret was about 1.0 mm and 0.15 mm/d, respectively. These rates are about twice the growth rates of age 0+ and 1+ pomfret estimated from otoliths (see Age and Growth section), and possibly result from size-selective migration of fish.

## II. Pomfret Distribution in Relation to Oceanography

Pacific pomfret are associated with the Transitional Domain of the Subarctic Water Mass during the summer months (Shimazaki and Nakamura 1981; Shimazaki 1989; Pearcy 1991). This region is located north of the prominent Subarctic Boundary (often defined by the vertical ascent or the surface intersection of the 34 ‰ isohaline) and south of the boundary between the Transitional and Central Subarctic Domains (where the 4°C isotherm plunges below 100 m) (Dodimead et al. 1963; Favorite et al. 1976). These two boundaries often coincide with strong latitudinal gradients of both temperature and salinity (Fig. 8), and with regions of relatively strong gradients in dynamic height and hence strong geostrophic currents (see Fig. 11E, 12E).

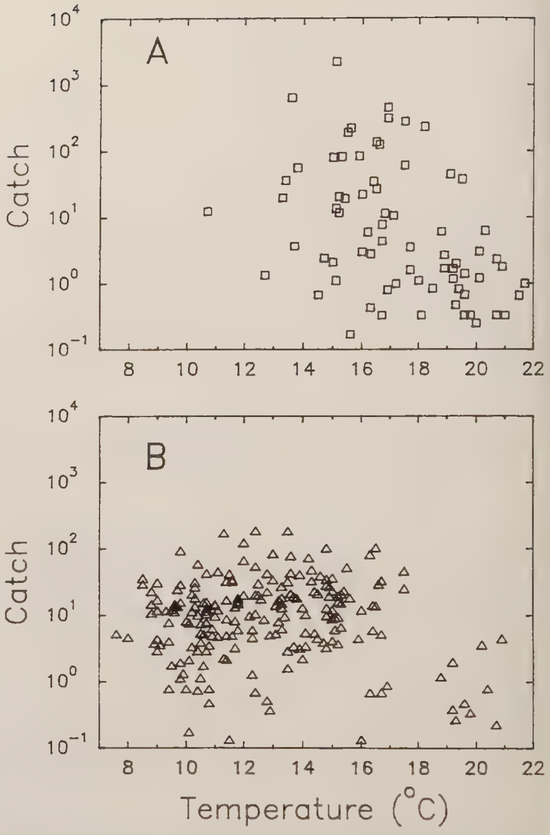

FIG. 10. Numbers of pomfret caught in the standard net vs. sea surface temperature for distinct modes of (A) small pomfret and (B) large pomfret.

### *Catches vs. sea surface temperature*

The mean lengths of pomfret varied with sea surface temperatures (Fig. 9). The mean size of small fish decreased with increasing temperature ($r = -0.62$; $P < 0.01$), as expected if migration to the north is size-dependent. No trend in mean size with temperature was apparent for the large fish ($r = 0.12$; $P > 0.05$).

Small pomfret were rarely caught in waters where the sea-surface temperature was less than 13°C, whereas large fish were commonly found where temperatures were from 8 to 13°C (Fig. 10). Thus the 13°C isotherm may be a boundary to the northward migration of small fish. During June and July, small pomfret inhabited waters over 4°C warmer than large pomfret (mean 17.3°C vs. 12.8°C).

Wada and Murata (1985) also reported size segregation of pomfret by temperature with large fish most numerous at surface temperatures of 13–17°C, while small fish were mainly found in 17–21°C water. Large fish were usually more common in waters

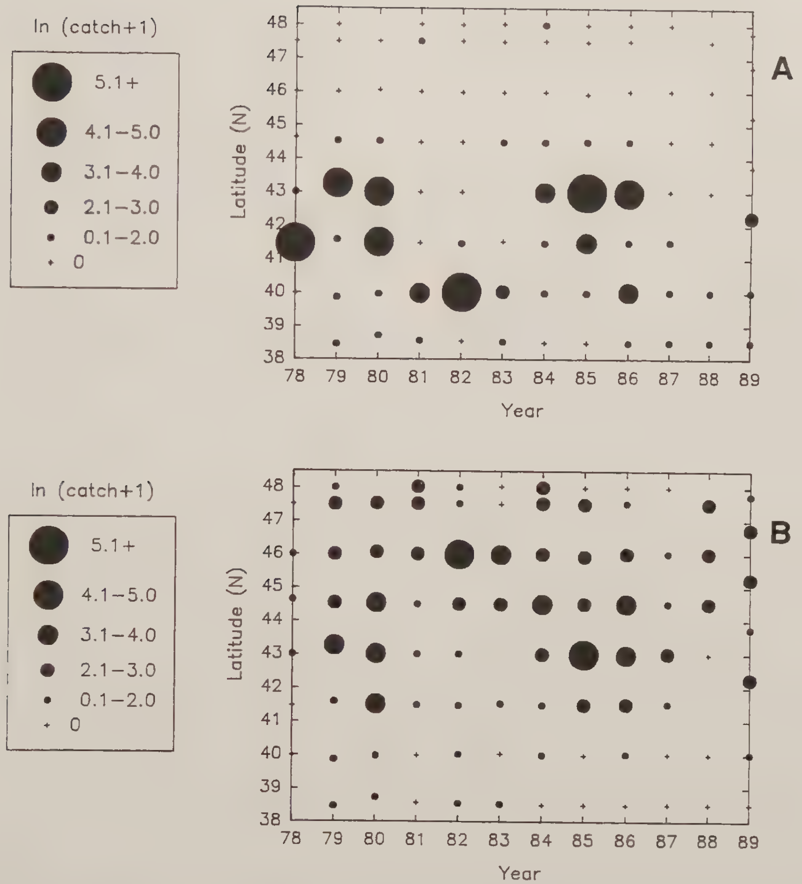

FIG. 11. Interannual variability along 175°E in the catches of (A) small (≤330 mm FL) and (B) large (>330 mm FL) pomfret, (C) sea surface temperature, (D) surface salinity, and (E) dynamic height of the sea surface relative to 700 m, the Subarctic Boundary (solid line) and the boundary between the Transitional and Central Subarctic Domains (dashed line). Stations along 175°E ± 2° of longitude are included. (*Fig. 11 concluded next page*)

with lower surface salinity, as expected in more northerly subarctic water. We found both large and small fish at higher temperatures (Fig. 10) than did Wada and Murata, probably because their collections were made in June whereas ours were made mainly in July.

Surface temperatures where pomfret were caught ranged from about 8° to 22°C, which is greater than the range reported by Hanavan and Tanonaka (1959), Neave and Hanavan (1960), and Hitz and French (1965). Machidori and Nakamura (1971) and Wada and Murata (1985) considered the 8.5–9.0°C isotherms to be close to the northern limit of distribution. We suggest that a surface temperature of 8.0°C is the thermal minimum for the occurrence of large Pacific pomfret. The southern limit of Pacific pomfret is associated with the 21°C isotherm (Mead 1972; Seki and Bigelow 1993), although we found small pomfret in water close to 22°C (Fig. 10).

### *Interannual trends in abundance*

Interannual variations in the catches of small and large pomfret in the standard net were compared for the two most complete north-south transects, 175°E and 170°E, 1978–89.

The number of small pomfret caught at different latitudes along 175°E varied from year to year. Catches extended north of 42°N during 1978 through 1980, retreated south of 42°N in 1981 and 1982 (except one fish at 47°30′N), and then moved to the north of 44°N during 1983 through 1986 and to the south of 43°N in 1987 and 1988 (Fig. 11A). These trends generally conform to variations in sea surface temperatures. Temperatures were warm north of 42°N during northern excursions of small pomfret and cool during the intervening years when abundances were high to the south (Fig. 11C). The 13–14° isotherms generally defined the northern limits of small pomfret along this transect during July. Surface salinity (Fig. 11D) and dynamic height (Fig. 11E) did not correlate as well as temperature with catch rates. High catch rates of small pomfret were usually located north of the 34 ‰ isohaline, either at the surface or where it was vertical at 100 m (i.e., the Subarctic Boundary), and south of the northern boundary of the Transitional Domain as indicated by the salinity

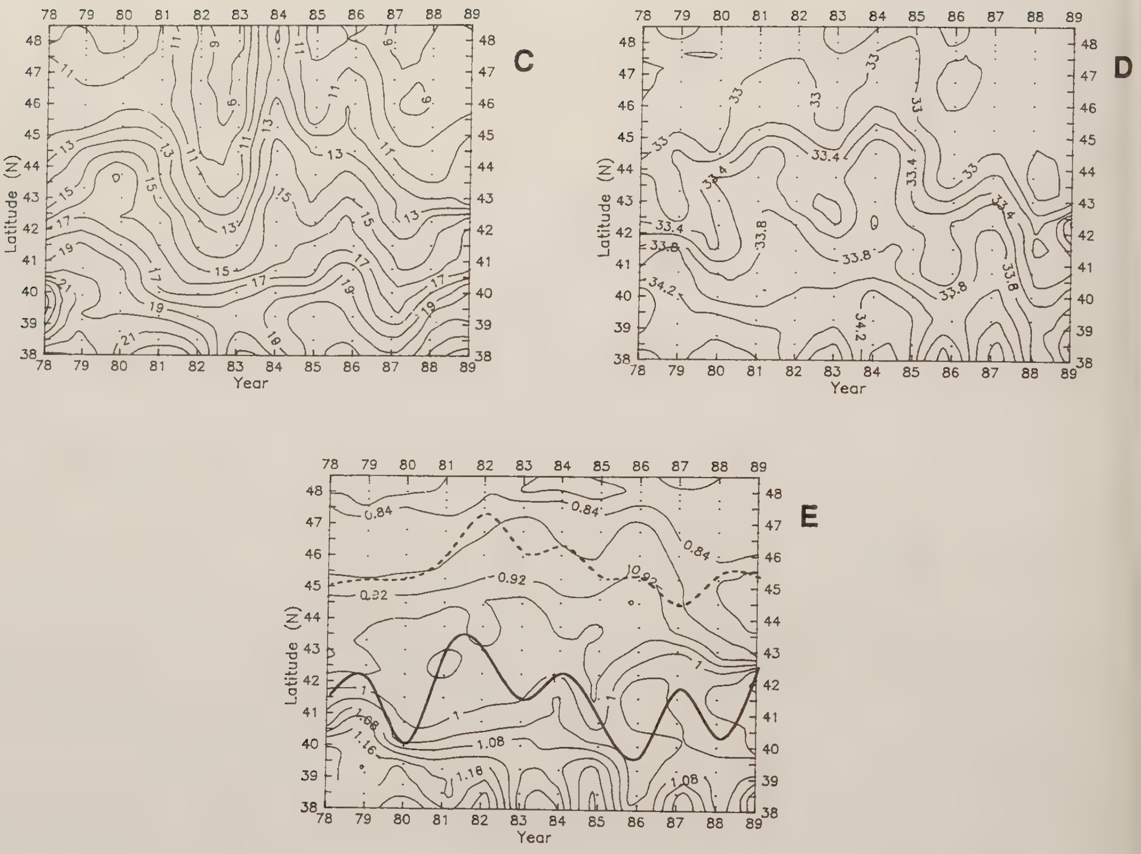

FIG. 11. *(Concluded)*

front centered between 33.2 and 33.4 ‰. During 1988 and 1989, when low surface salinities dipped to the south and strong currents were located at mid-latitudes (42–43°N) the catches of small pomfret were low at all latitudes.

Large pomfret along 175°E were distributed much farther to the north than small pomfret (Fig. 11A,B). However, both large and small pomfret were abundant at the same latitudes north of 42°N during 1980 and 1985–86. During 1982 and 1983, on the other hand, when small fish retreated to the south and sea surface temperatures declined, the highest catches of large pomfret were made at 46°N, in waters where surface temperatures were 9–10°C (Fig. 11C). This suggests that large pomfret are more eurythermal than small pomfret. Large pomfret often were common north of the front between the Transitional and Central Subarctic domains, and within the salinity front and region of accelerated currents (Fig. 11D,E).

Catch rates of small pomfret along 170°E were highest between 40° and 42°N during 1981–82 and 1984–85 (Fig. 12A), when warm surface temperatures bulged northward (Fig. 12C) and when the Subarctic Boundary extended northward (Fig. 12D). Catches were low during 1983, when low sea surface temperatures (13°C) intruded south of 41°N (Fig. 12C). Catches were generally low at all latitudes during 1986–1989, a period when unusual ocean conditions were not evident. These interannual trends have similarities to those at 175°E. Again, small pomfret were confined to waters south of the salinity front and accelerated currents associated with the northern boundary of the Transitional Domain.

High catches of large pomfret extended farthest to the north during 1984 (Fig. 12B), when warm surface waters (>10°C) occurred as far north as 47°30′N (Fig. 12C). Wada and Murata (1985) also found interannual variations in the size distribution of pomfret off northern Japan. In some years, such as 1980, the small size mode predominated in the catches. Fluctuations in the relative abundance of small pomfret suggest year-to-year variations in the year-class strength and recruitment of 0-age pomfret.

### *Catches in the Gulf of Alaska*

Small pomfret were much less common in the eastern than the western North Pacific during July. In contrast with transects to the west, distinct modes of small pomfret were evident from size distributions of only four sets between 38°–42°30′N along 155°W (Fig. 4). Modes of small fish were not evident in the numerous sets farther to the east in the Gulf of Alaska, although a few small pomfret sometimes made up the tail end of the size distribution of the large mode.

High catches of large-sized pomfret were made during July in the Gulf of Alaska, especially from 48°–50°N along 145°W, from

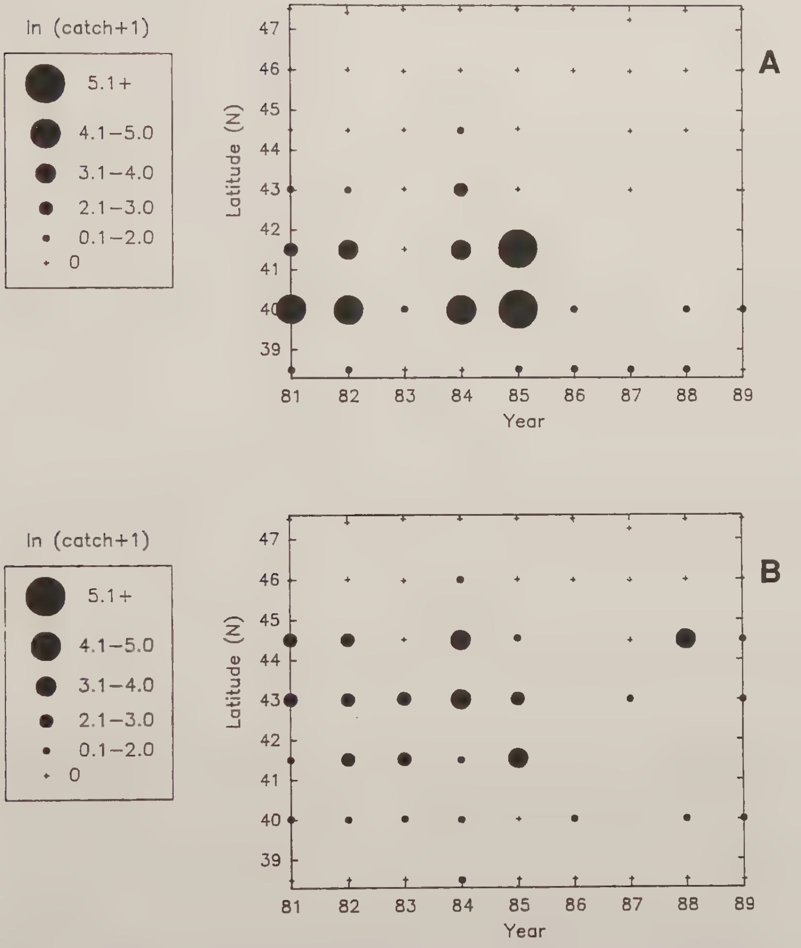

FIG. 12. Interannual variability along 170°E in the catches of (A) small (≤330 mm FL) and (B) large pomfret (>330 mm FL), (C) sea surface temperature, (D) surface salinity, and (E) dynamic height of the sea surface relative to 700 m and the Subarctic Boundary (solid line) and the boundary between the Transitional and Central Subarctic Domains (dashed line). Stations along 170°E ± 2 longitude were included. (*Fig. 12 concluded next page*)

136°–141°W along 55°N, and 52°–54°N along the coast of British Columbia (Fig. 13). Large pomfret were found in all but one set east of 141°W. The higher catches of pomfret in the eastern than the western Gulf of Alaska north of 50°N were associated with relatively high temperatures compared to waters at the same latitude to the west (11.4–12.0° vs. 8.7–10.7°C during 1982 and 13.6° vs. 10.4–11.8°C during 1983 along 55°N). These relatively warm temperatures in the eastern Gulf of Alaska may be associated with the Alaska Current.

Although sea surface temperatures in the region of low catches were lower than those farther to the east, they were always above the thermal minimum for large fish (Fig. 10). Surface temperatures at stations of zero catches were below 9°C at only 9 of 44 stations. These low or zero pomfret catches occurred in the region of the Alaska Stream at the northern stations along 155°W and where isotherms dome near the center of the Alaska Gyre (Ridge Domain) farther to the east (see Pearcy et al. 1988). Hitz and French (1965) also caught few pomfret in numerous gillnet and purse seine sets between 140°–149°W and north of 54°N in the Gulf of Alaska, but they did catch pomfret north of 55°N along 150°W. These trends suggest a possible discontinuity in the distribution of Pacific pomfret between the eastern and western Gulf of Alaska.

### III. Patchiness within Gill Nets

Coefficients of dispersion of the number of pomfret caught in

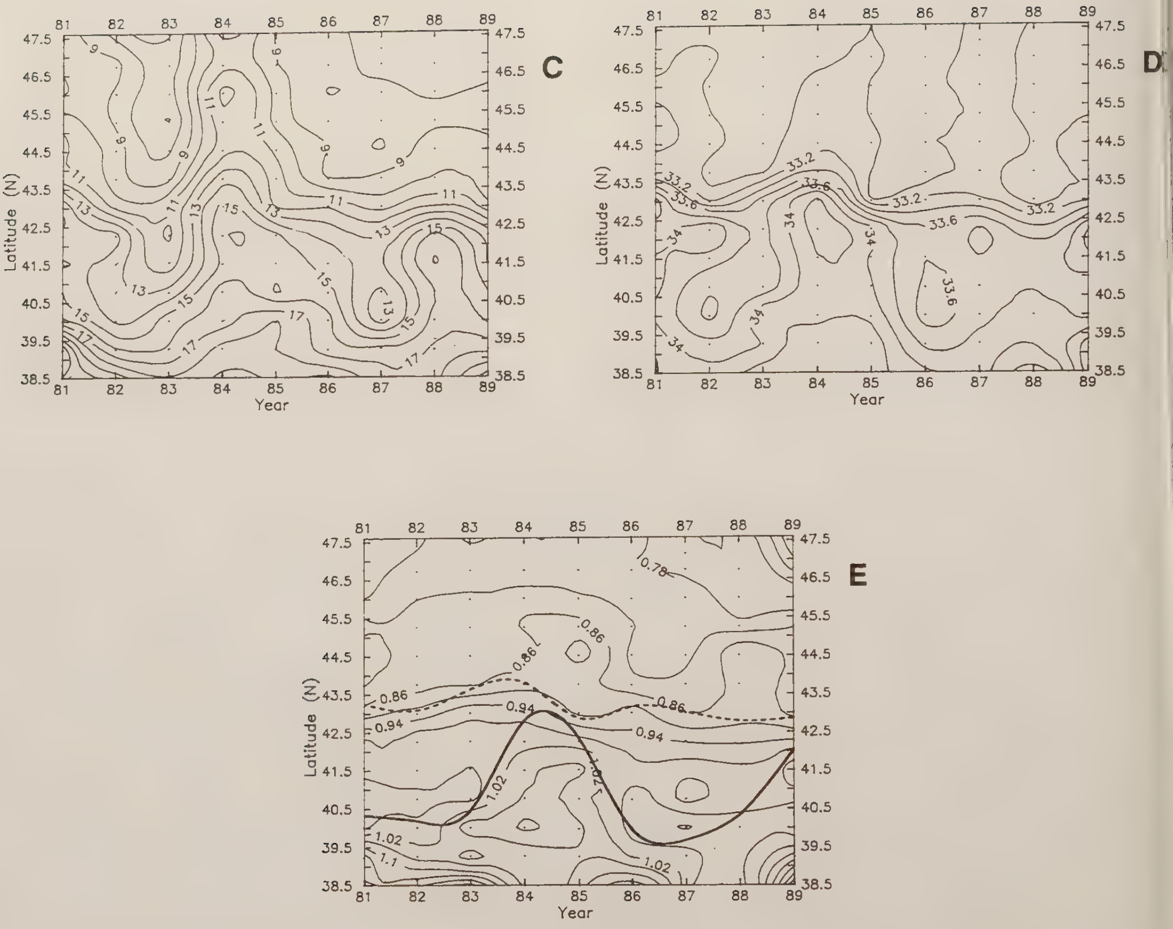

FIG. 12. (*Concluded*)

contiguous tans of the same mesh were, with one exception, close to 1.0 (0.87–3.0), for 26 comparisons. Low coefficients indicate that pomfret did not form compact aggregations or schools on a scale of a kilometer or less, but were randomly dispersed near the surface at night when they were entangled in the gill nets. Interception of many small schools at different times during the night could increase the impression of randomness. Conversely, patchiness could occur at large spatial scales that would not be detected.

## IV. Age and Growth

Ages of 184 Pacific pomfret, from 211 to 500 mm FL, ranged from 0+ (young-of-the-year) to 6+ years (fish in the seventh year of life) based on otoliths. All otoliths had an opaque band of relatively rapid growth along the edge, as expected because fish were collected during summer. This was reported as "+" following the estimated age. The age of small fish was estimated from 49 whole otoliths, and confirmed by 18 sagittal or transverse sections. Ages of young-of-the-year Pacific pomfret estimated from sections and from whole otoliths did not differ. All otoliths having a surface age over 2 yr were sectioned (Fig. 14).

Pacific pomfret grow rapidly during their first 2 yr of life (Fig. 15). Growth was described with a von Bertalanffy function:

$$l_t = L_\infty (1 - e^{-k(t-t_0)}),$$

where $L_\infty$ was estimated at 468 mm FL, $k$ was 0.76 and $t_0$ was $-0.52$ yr. Lengths of our 6+ yr-old fish (i.e., 494 and 500 mm FL) were above the asymptote of the fitted curve, which underestimated the maximum length of pomfret. Although Pinckard (1957) suggested that Pacific pomfret reach a total length of 1220 mm, the largest previously reported sizes were 500–550 mm FL (Wada and Murata 1985). In this study, only 26 fish >500 mm FL and three fish >600 mm FL were measured. The largest was 614 mm FL, suggesting a maximum size of about 600–620 mm FL.

Our estimates of size-specific age agree with those based on annuli-like structures on scales from the caudal peduncle through age 3 (Shimazaki 1989). He reported fork lengths of 180–240 mm for age 0+, rapid growth to 360–400 mm by age 1+, and then slower growth to 380–480 mm for fish of age groups 2 and 3. However, he did not find annuli-like patterns on

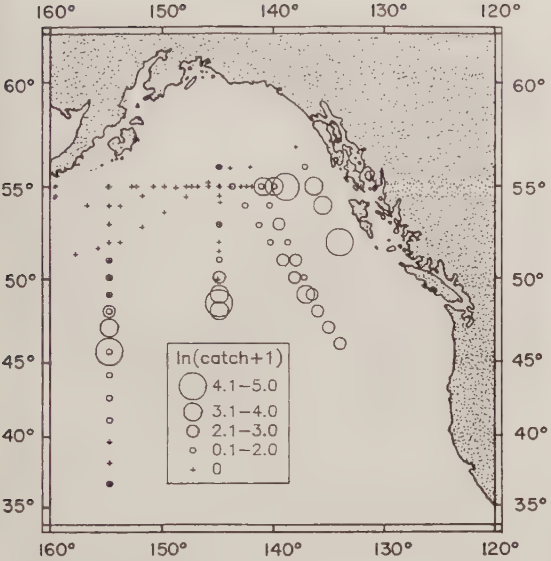

FIG. 13. Catches of large pomfret in the standard net in the Gulf of Alaska for all years.

TABLE 1. Food items identified from the stomachs of Pacific pomfret in the Gulf of Alaska and along 180°.

| | Gulf of Alaska | 180° |
|---|---|---|
| Euphausiids | | |
| *Thysanoessa spinifera* | × | |
| *Euphausia pacifica* | × | |
| *Gnathophausia* | × | |
| Amphipods | | |
| *Cystisoma* | × | × |
| *Phronima* | × | × |
| *Themisto* | × | |
| Shrimp | | |
| *Sergestes similis* | × | |
| Barnacles | | |
| *Lepas* | | × |
| Pteropods | | |
| *Euclio* | | × |
| Heteropods | × | |
| *Carinaria* | × | × |
| Squids | | |
| *Berryteuthis anonychus* | × | |
| *Gonatus* | × | × |
| *Chiroteuthis* | × | |
| *Onychoteuthis* | × | |
| Fishes | | |
| *Tarletonbeania* | × | × |
| Myctophids | | × |
| *Lestidiops ringens* | × | |
| *Hemilepidotus* | × | |
| *Pleurogrammus monopterygius* | | × |
| *Cololabis saira* | | × |
| *Sebastes* | × | |

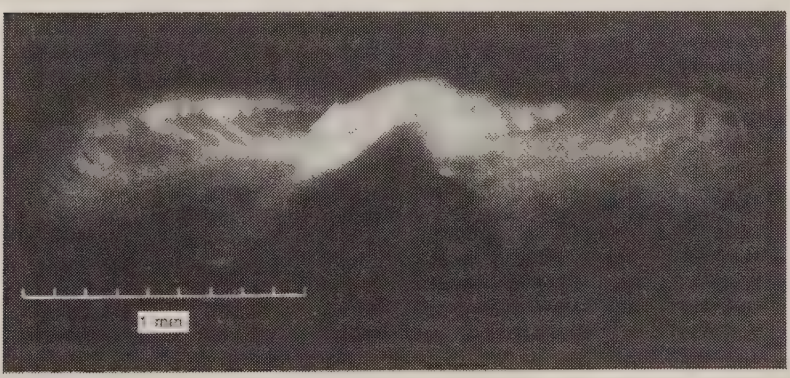

FIG. 14. Transverse section of an otolith of a Pacific pomfret, 494 mm FL. Age is estimated at 6+ yr, each yearly increment denoted by a dark line.

scales indicating age groups older than 3 yr, or minute growth increments in otolith sections indicating ages over 2 yr. Thus Shimazaki's estimates suggest that Pacific pomfret grow rapidly to 400–500 mm FL in less that four years, similar to our estimates based on otoliths.

Both our estimates and Shimazaki's differ from the much slower growth suggested by Machidori and Nakamura (1971). From otoliths and length frequencies they estimated that fish of two modal fork lengths groups, 350 and 405 mm, were age 4 and 5, respectively. Thus, we explain the absence of intermediate size modes (290–350 mm FL, Fig. 2) of Pacific pomfret during spring and summer surveys, ascribed previously to inadequate areal coverage or selectivity of gear (see Wada and Murata 1985), by the rapid growth of age 0+ fish to a large mode of slower growing fish, with intermediate sizes (300–350 mm FL) present only in the fall and winter. Based on our growth curve (Fig. 15), small fish (≤330 mm FL) in our catches were age 0+ and large fish (331–500 mm FL) were ages 1+ to 6+.

The number of fine-scale increments in sagittal sections of otoliths corroborate the rapid growth of young pomfret. Otoliths

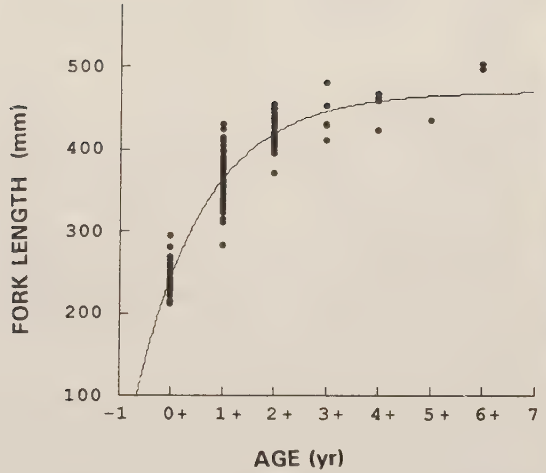

FIG. 15. Estimated age vs. fork length for Pacific pomfret. The line is a von Bertalanffy growth equation ($l_t = L_\infty (1 - e^{-k(t-t_0)})$) fitted to these estimates.

from 0+ fish (200–260 mm FL) had 130–221 increments. Number of increments was positively correlated with fork length ($r$ = 0.63). Assuming these are daily increments, hatch dates ranged from January to April. This supports the findings of Shimazaki (1989) that small pomfret (200–250 mm FL) caught in late July had less than 160-min growth increments, indicating than they hatched during February, again assuming that these increments are daily. Similarly, larval and juvenile pomfret caught in early March near the Hawaiian Archipelago were estimated to have hatched during January based on otolith microstructure (Seki and Bigelow 1993). It should be noted that none of the methods for ageing Pacific pomfret has been validated.

Rapid growth early in the life history of pomfret is similar to that of other epipelagic fishes, such as juvenile sablefish (*Anoplopoma fimbria*), a subarctic fish that is pelagic during its first year of life (Boehlert and Yoklavich 1985). Albacore (*Thunnus alalunga*), a highly migratory epipelagic fish of transitional waters, also has rapid growth during the first three years of life (Beamish 1981).

## V. Food Habits

Pacific pomfret prey include a variety of pelagic crustaceans, mollusks, and fishes (Table 1). Gonatid squids were common in stomachs collected in the Gulf of Alaska where they dominated the stomach contents at 24 of 28 stations and usually comprised 75% or more of the prey (Table 2A,B,C,D,G). When squids were principal prey, the percentage of empty stomachs was usually low and stomach fullness was high.

Small *Gonatus* spp. squids (dorsal mantle length-DML <60 mm) were most important in the northern Gulf of Alaska where cold, saline waters protrude toward the surface (i.e., the Ridge Domain of Favorite et al. (1976)) and waters of the Alaska Current (55–53°N), whereas larger (DML >70–80 mm) *Berryteuthis anonychus* comprised most of the squid biomass consumed farther to the south in the region of the Subarctic Current (52–49°N). This species was the primary prey and contributed to the high stomach fullness of pomfret, as well as salmonids (Pearcy et al. 1988), in this region. Even farther to the south (48–44°N), in the Transitional Domain, other small squids (often gonatids) were present in pomfret stomachs but were of lesser importance. Gonatid squids were identified from pomfret caught along 180°, but no *B. anonychus* were found.

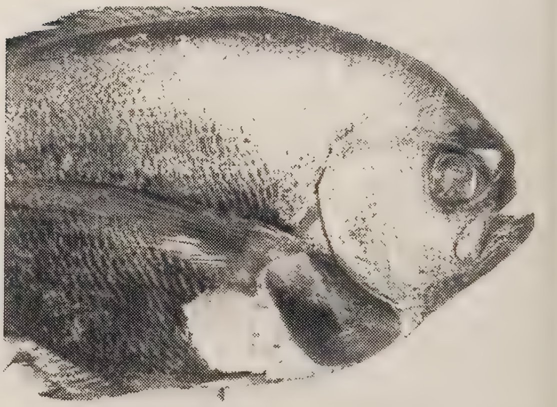

FIG. 16. Photograph of pomfret with skin removed from pectoral girdle and posterior area showing the dark coloration of the musculature of the lateral muscles associated with the pectoral fin.

In our study, euphausiids were the major prey for large pomfret only at one station (50°N) in the Gulf of Alaska and at two stations along 180° (Table 2E,F,G). Pteropods were only found in fish from stations along 180°, but are sometimes important as food for epipelagic fishes in the subarctic eastern Pacific (Pearcy 1991). Among fishes found in pomfret stomachs, the myctophid *Tarletonbeania crenularis* occurred most frequently in the Gulf of Alaska (north of 45°N) and along 180°. The slender barracudina, *Lestidiops ringens*, occurred only in stomachs from the Gulf of Alaska, and the Pacific saury (*Cololabis saira*) was only found along 180° (Table 1).

Other investigators found that squids were important prey for large pomfret in the Gulf of Alaska, as elsewhere in the Central Subarctic Pacific (Pinckard 1957; Machidori and Nakamura 1971; Wada and Murata 1985; Shimazaki 1989). Shimazaki and Nakamura (1981) reported that squids and fishes were the most frequent food items for large pomfret during most months of the year. Kubodera and Shimazaki (1989) found that the gonatids (*Gonatus middendorffi*, *G. berryi*, and *G. pyros*) were more numerous than *B. anonychus* in stomachs of large pomfret caught west of 175°W. This is explained by the more easterly distribution of *B. anonychus* in the subarctic Pacific (Kubodera and Jefferts 1984; Kubodera and Shimazaki 1989).

Crustaceans were important prey for small pomfret off Japan during June (Wada and Murata 1985) and for large pomfret during the winter south of the Subarctic Boundary (Shimazaki and Nakamura 1981; Seki and Bigelow 1993). Euphausiids were important in the spring when other prey items were less abundant (Shimazaki 1989).

Shimazaki and Nakamura (1981) found that stomach fullness of Pacific pomfret was highest in the Subarctic Domain, where the catch per effort in gill nets was the highest, and decreased markedly to the south in the transition and subtropic regions. This high availability of pomfret prey in northern waters during the summer results in a 30% increase in body weight compared to that in the winter (Shimazaki 1989). Pomfret not only take advantage of increased secondary production of food in subarctic waters during the summer, but also follow small migratory fishes such as Pacific saury, sardine, and Pacific mackerel northward during the summer (Taniguchi 1981; Shimazaki 1986).

In the western Pacific, fishes rather than squids are often reported as the most important prey taxon for pomfret. Here the Japanese sardine (*Sardinops melanostictus*) was often the principal prey of large pomfret (Kohno 1983; Wada and Murata 1985), but in 1991, following a decline in Japanese sardine, pomfret fed on Japanese anchovy (*Engraulis japonicus*) and squids (Wada and Honda 1992), demonstrating their opportunistic feeding behavior.

## VI. Parasites, Predators, and Populations

The only large parasite found in the flesh of pomfret was the larval stage of the trypanorynch tapeworm *Molicula* sp., that burrows into the muscle of the fish and eventually reproduces in the digestive tract of its final host. Two and one-half times more larval *Molicula* were found in pomfret caught in the western than the eastern Pacific (mean (std. dev.) 4.3 (2.53)) tapeworms per fish vs. 1.7 (1.4); $P < 0.005$).

These observations on parasites are important for two reasons. First, because all adult trypanorynchs occur only in elasmobranchs (Rohde 1984), sharks may be the major predator of Pacific pomfret. The blue shark and the Pacific pomfret have broadly overlapping distributions in the Transitional Domain of the subarctic Pacific during the summer (Mishima 1981; Pearcy 1991). Pomfret remains have been reported in the stomachs of the blue shark (*Prionace glauca*) in the Gulf of Alaska (LeBrasseur 1964), and in the Subarctic Frontal Zone north of the Hawaiian Islands (Seki 1993).

Second, this difference in parasite loads, as well as postulated differences in the spawning season of Pacific pomfret in the eastern and western Pacific, the absence of distinct modes of small pomfret in the eastern Gulf of Alaska, and the hiatus in distribution of large pomfret in the central Gulf of Alaska, all suggest geographic differences in stock structure.

Yoon and Shimazaki (1981) reported seasonal peaks in the gonosomatic indices that suggested the main spawning season of Pacific pomfret was early June and July between 140–177°W and during the winter and early spring (December–April) farther to the east (160–170°E) (see also Shimazaki 1989; Seki and Mundy 1991). The few data on the occurrence of larval and juvenile pomfret, however, indicate that the subtropic region in the mid-Pacific (29°47′N, 179°E) is a winter spawning area (Seki and Mundy 1991). At 28°N, 155°W, Loeb (1979) collected 49 larval pomfret during January–February and three during September, again suggesting primarily winter spawning in this region. These studies suggest that pomfret spawn during the winter in the central and eastern Pacific, not during June and July as postulated by Yoon and Shimazaki (1981).

Farther to the east in the southern region of the California Current (ca. 27–35°N and east of 125°W), *Brama* spp. larvae are rare (Stevens et al. 1990), but *B. japonica* larvae were collected during most months of the year, indicating year-around spawning, with the highest average abundance during October–December (G. Moser personal communication). Four of the five Pacific pomfret caught by Berry and Perkins (1966) off California (30°07′–34°47′N, 124°31′–129°16′W) appeared to be from spawning in the winter (15.5 mm standard length (SL) in March and 215–220 mm SL (similar to our age 0+) during August). However another specimen of 52.5 mm SL was collected during August, suggesting spring spawning. Thus it seems premature to conclude that Pacific pomfret has different spawning seasons in the eastern and western Pacific. We agree with Shimazaki (1989) that more research is needed on the seasonality of spawning and occurrence of eggs and larvae of Pacific pomfret to determine the existence of separate populations in the North Pacific.

## VII. Swimming Behavior

During several cruises of the Oshoro Maru, it was noted that Pacific pomfret caught in gill nets set overnight and retrieved during the early morning were always dead, whereas other fishes (e.g., salmonids), were sometimes alive. This observation led to the hypothesis that Pacific pomfret swim continuously to ventilate their gills, and that entanglement in gill nets interferes with respiration and causes death. To test this idea, live pomfret were observed in tanks with running sea water aboard the ship.

Pacific pomfret (35–40 cm FL) swam continuously in tanks at speeds of about one body length per second. Propulsion was exclusively by their long, falcate pectoral fins (34–38% of standard length; Mead 1972) that flapped in unison about once per second. The forces of buoyancy and lift were about equal because the axis of body motion was nearly horizontal during pectoral swimming. The pectorals were also used to dive rapidly and to change vertical position in the tank. The caudal fin was used to accelerate and to turn at the ends of the tank. Bending of the relatively rigid dorsal and anal fins was also observed during turns, but these fins did not flap. Pomfret were very maneuverable and seldom collided with the walls of the tank. Their maneuverability in nature may assist in capturing squids which accelerate rapidly.

At swimming speeds of about 30–40 cm/s, the mouth was open and the opercle was slightly open. Opercular pumping was not seen. These observations indicate ramjet ventilation of the gills. Gape distance appeared to vary inversely with swimming speed. However, two fish that were on their sides on the bottom of the tank remained alive after 24 h and used opercular pumping to ventilate their gills. This suggests that ramjet ventilation is not obligatory, and that the death of Pacific pomfret in gill nets was due to interference with opercular movements, as well as prevention of ramjet ventilation, their normal means of gill ventilation.

Dissection of several fish at sea revealed that both the abductor and adductor muscles of the pectoral fin consisted of dark red muscle fibers, presumably enriched in capillaries and myoglobin. Red muscle is used for continuous propulsion in other fishes (Webb 1975). These dark red muscles contrasted with the white muscle fibers seen throughout the rest of the body (Fig. 16). No red muscle was associated with the lateral muscle mass of the body as in tunas and other fast swimming pelagic fishes.

Pectoral fin muscles of one specimen (355 mm FL, 759 g total weight) were dissected and weighed. The paired abductors (superficialis and profundus) located on the lateral face of the pectoral girdle (see Winterbottom 1974 for muscle morphology)

TABLE 2. Food habits of pomfret collected in the Northeast Pacific from the T/V *Oshoro Maru*, 1980–87. (A) percent of wet-preserved weights of taxa, (B) percent frequency of occurrence, and (C–G) percent by volume.

A. 1980, along 145°W

| | Latitude north | |
|---|---|---|
| | 50° | 48°30′ |
| Euphausiids | 0 | 2 |
| Amphipods | 0 | T |
| Squids | 86 | 91 |
| Fishes | 4 | 3 |
| Unidentified | 10 | 5 |
| No. examined | 10 | 50 |
| % empty | 10 | 20 |

D. 1985, along 155°W

| | Latitude north | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 48° | 47° | 45°30′ | 44° | 42°30′ | 41° | 39°30′ | 38° | 36°30′ |
| Squids | 98 | 100 | 95 | 100 | 100 | 5 | | | 58 |
| Fishes | 2 | 0 | 5 | 0 | 0 | 21 | | | 38 |
| Other | 0 | 0 | 0 | 0 | 0 | 74 | | | 5 |
| No. examined | 38 | 20 | 30 | 6 | 1 | 25 | 0 | 0 | 6 |
| % empty | 0 | 5 | 10 | 17 | 0 | 40 | | | 33 |
| Fullness | 2.9 | 3.0 | 2.2 | 2.2 | 1.0 | 1.3 | | | 2.0 |

B. 1981, along 145°W

| | Latitude north | | |
|---|---|---|---|
| | 51° | 50° | 49° |
| Amphipods | 0 | 5 | 8 |
| Squids | 88 | 69 | 90 |
| Fishes | 38 | 0 | 6 |
| No. examined | 8 | 42 | 50 |
| % empty | 0 | 12 | 2 |
| Fullness | 1 | 2 | 2 |

E. 1986, along 180°

| | Latitude north | | | | | |
|---|---|---|---|---|---|---|
| | 37° | 38° | 39° | 40° | 41° | 42° |
| Euphausiids | 11 | 24 | 26 | 59 | 34 | 4 |
| Amphipods | 0 | 4 | 2 | <1 | 16 | 8 |
| Squids | 11 | 15 | 1 | 7 | 17 | 35 |
| Fishes | 78 | 38 | 36 | 23 | 16 | 46 |
| Other | 0 | 18 | 35 | 11 | 18 | 6 |
| No. examined | 26 | 23 | 31 | 27 | 28 | 27 |
| % empty | 34 | 4 | 22 | 4 | 11 | 7 |
| Fullness | 2.4 | 1.9 | 2.1 | 1.9 | 1.3 | 1.8 |

C. 1984, along 155°W

| | Latitude north | | | | |
|---|---|---|---|---|---|
| | 49° | 48° | 47° | 45° | 44° |
| Euphausiids | 0 | 0 | <1 | 0 | 0 |
| Amphipods | 0 | 0 | 7 | 15 | 2 |
| Squids | 92 | 64 | 80 | 73 | 23 |
| Fishes | 8 | 36 | 5 | 7 | 50 |
| Other | 0 | 0 | 7 | 5 | 25 |
| No. examined | 14 | 25 | 30 | 30 | 33 |
| % empty | 14 | 60 | 13 | 33 | 36 |
| Fullness | 3.43 | 0.8 | 2.53 | 0.5 | 1.5 |

F. 1987, along 180°

| | Latitude north | | | |
|---|---|---|---|---|
| | 39° | 40° | 41° | 42° |
| Euphausiids | <1 | 53 | 12 | 11 |
| Amphipods | 0 | 9 | 3 | 0 |
| Squids | 12 | <1 | 25 | 74 |
| Fishes | 72 | 37 | 36 | 10 |
| Other | 5 | 9 | 25 | 5 |
| No. examined | 20 | 58 | 39 | 10 |
| % empty | 60 | 16 | 48 | 0 |

G. 1987, on a diagonal from 56°N to 45°59′N

| | Latitude north, longitude west | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 56°00′ 145°00′ | 55°00′ 143°48′ | 54°00′ 142°38′ | 52°27′ 141°23′ | 52°60′ 140°20′ | 51°00′ 139°12′ | 50°00′ 138°08′ | 49°00′ 137°05′ | 48°00′ 136°00′ | 47°00′ 135°00′ | 45°59′ 133°58′ |
| Euphausiids | 0 | 27 | 0 | <1 | 0 | 0 | 60 | 0 | 0 | <1 | 0 |
| Squids | 47 | 68 | 95 | 66 | 100 | 75 | 32 | 62 | 74 | 97 | 91 |
| Fishes | 53 | 5 | 2 | 5 | 0 | 25 | 8 | 16 | 12 | 2 | 9 |
| Other | 0 | 0 | 3 | 29 | 0 | 0 | 0 | 22 | 14 | <1 | 0 |
| No. examined | 3 | 23 | 28 | 30 | 11 | 29 | 30 | 35 | 31 | 31 | 32 |
| % empty | 0 | 17 | 4 | 30 | 18 | 58 | 60 | 17 | 16 | 26 | 66 |
| Fullness | 1.0 | 1.7 | 1.8 | 1.3 | 2.9 | 1.6 | 1.5 | 2.3 | 1.6 | 1.2 | 1.4 |

had about the same mass as the adductor muscles on the medial face of the pectoral girdle. The combined weight of these muscles (9.8 g) from one pectoral girdle was 4.5% of the combined white (210 g) and red muscles mass from the same side of the body. This is about the same ratio of red muscle to total musculature reported for the labrid *Oxyjulis californica*, that relies on pectoral fins for normal swimming (Rosenblatt and Johnson 1976), but less than the ratio of red to white muscles found in myotomal musculature of rainbow trout (*Oncorhynchus mykiss*) (Webb 1971) and of red muscle to body mass in most of the scombrids studied by Magnuson (1973). It is far less than the ratio reported for the ocean opah (*Lampris guttatus*), that swims with its comparatively short pectoral fins and has large red adductor and abductor muscles comprising 37% of the total propulsive musculature (Rosenblatt and Johnson 1976).

## Conclusions

Pacific pomfret has attracted attention as an underutilized resource because of its high abundance in fisheries for other species. Often it is the dominant nonsalmonid fish in gill net and purse seine catches in the subarctic region during the summer (Neave and Hanavan 1960; Hitz and French 1965; Machidori and Nakamura 1971; Yatsu et al. 1993). High abundance throughout much of the epipelagic waters of the North Pacific, rapid growth rate, and segregation of large and small individuals during northward migrations are favorable characteristics of a potentially productive fishery. In addition, we found no decrease in either catch per standard set of large pomfret or mean size of pomfret during our study that was coincident with the large-scale drift net fishery for flying squid. This indicates that the population of Pacific pomfret had not been adversely affected by its incidental catch in the flying squid fishery.

Although much is known about the biology of pomfret (see Shimazaki 1989), important features of their biology and ecology need to be evaluated. Differences in parasite loads and age structure suggest different stocks in the eastern and western North Pacific. The discreteness of stocks is an important management consideration and should be resolved, possibly by biochemical or genetic studies or larval surveys, before intensive exploitation.

Reliable methods of ageing need to be further developed, including an age-specific study to validate growth increment periodicity. Age determination is vital to estimates of growth, mortality, age at first spawning, and ages of large and small fish during the summer season. Information on reproduction in the Northeast Pacific is also needed.

Little is known about the early life history of Pacific pomfret, and nothing about factors affecting survival and year-class success. Better understanding also is needed on the role of Pacific pomfret in the North Pacific pelagic ecosystem and how a fishery would affect other species, including salmonids.

Finally, fishing techniques to catch pomfret may be problematical. Drift gill nets are not an acceptable option unless bycatch of other species is minimal. To target pomfret with purse seines or trawls, more information is needed on gear selection, schooling behavior, and oceanographic and geographic factors that may result in dense, available concentrations.

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# Biological observations from the Cobb Seamount rockfish fishery

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The Cobb Seamount was discovered in 1950 by the crew of the fishery research vessel *John N. Cobb* (Anonymous, 1950). This submerged volcanic mountain (Budinger, 1967) is located approximately 280 nautical miles (nmi) off the southern Washington coast and comes to within 50 meters of the sea surface. At the 200-m isobath, its area is approximately 32 nmi$^2$ (Budinger, 1967). Various efforts have been made to study the biological, oceanographic, and geologic characteristics of the seamount since its discovery (Budinger, 1967; Birkland, 1971; Dower et al., 1992), but these efforts have been somewhat limited in scope and duration. The studies have shown that the seamount has concentrations of commercially valuable species including rockfishes (genus *Sebastes*). Most of the information about commercial fishing operations on the seamount is anecdotal and speculative, primarily because the seamount is located outside the Exclusive Economic Zone (EEZ) and therefore fishing vessels operating there are not subject to fishing regulations or routine sampling. What is known, however, is that bottom trawl, midwater trawl, gill net, and longline fishing has occurred at various times.

Foreign and domestic fleets have fished on the Cobb Seamount from at least the mid 1960's (Sasaki, 1986). Most of the fishing operations appear to have been aimed at several species of rockfish. Sasaki (1986) suggests that prior to 1985, there was intense fishing pressure on the seamount by the Japanese fishing fleet. In 1985, a few fishermen from Oregon attempted to trawl on the Cobb Seamount but were unsuccessful. It is not known why these efforts failed. Little fishing activity is believed to have occurred on Cobb Seamount between 1985 and September 1991.

In 1991, fishermen from Oregon and Washington returned to Cobb Seamount; this time they were successful. This success drew the attention of fishery managers because fish caught outside the EEZ are not regulated by the west coast Fisheries Management Plan governing nearshore stocks. Because of the regulatory problems presented by this new fishery, port samplers were instructed to give a high priority to sampling of landings from Cobb Seamount in part as an effort to identify any unusual characteristics which might make landings identifiable. In this paper we present some of the unique characteristics of the fish populations found on Cobb Seamount, particularly widow rockfish (*S. entomelas*). This seamount is isolated enough from coastal fish populations so that recruitment dynamics, density dependent growth, and bioenergetic studies could provide valuable new insights into fisheries biology.

## Methods

Landings of commercially important groundfish are routinely sampled by biological technicians in Oregon according to standard protocols. Landings of fish from Cobb Seamount were sampled by port samplers in Oregon at two or three times the normal level and the majority of landings were sampled. All samples of widow rockfish were taken from vessels by using midwater trawl gear with the same mesh size as used in the nearshore widow rockfish fishery. During a four-month period, 11 landings were sampled by taking multiple 50-pound subsamples from each landing. Fork lengths were obtained from 891 widow rockfish, otoliths were removed from 724 of these fish for age determination by the broken and burnt method (Chilton and Beamish, 1982).

Mean length-at-age, age composition, and physical characteristics of the otoliths were compared to samples collected from landings of widow rockfish caught in the nearshore areas of the northern Oregon-southern Washington coast. To eliminate yearly and seasonal bias, comparisons of nearshore widow rockfish to Cobb Seamount widow rockfish were limited to the same months and years for both groups. To compare mean length-at-age of Cobb widow rockfish to the nearshore widow rockfish, only six-year-old fish could be used because of the small number of fish in other

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age groups for both areas. Otoliths were visually inspected without a microscope to look for gross morphological differences.

## Results and discussion

Several unique features were observed in the landings of widow rockfish from Cobb Seamount. Mean length-at-age was similar for six-year-old widow rockfish in both areas; however, size composition, age composition, and physical structure of the otoliths were very different between the two areas.

Mean length of six-year-old widow rockfish on the Cobb Seamount was 35.3 cm FL ($n$=72, SE=0.11) and 37.3 cm FL ($n$=140, SE=0.09) for males and females, respectively. In the nearshore samples, the mean length of six-year-old fish was 35.3 cm FL ($n$=53, SE=0.22) and 37.8 cm FL ($n$=52, SE=0.26) for males and females, respectively. This suggests that mean length-at-age, at least for young fish, is similar between fish caught on the Cobb Seamount and fish caught in the nearshore area. Assuming that the fish on the seamount spent the majority of their lives there, then it is reasonable to assume that conditions affecting growth (temperature, food availability, competition, etc.) are probably comparable to the conditions found in the nearshore environment.

In the northern Oregon-southern Washington area of the Pacific coast, the mean length of widow rockfish in the commercial landings is 38.4 cm (Pearson and Hightower, 1991). In contrast, the mean length of widow rockfish from Cobb Seamount was 33.1 cm. Age composition of the widow rockfish in the landings from the Cobb Seamount is also very different from those in the landings from the nearshore area (Fig. 1). Only 7.5% of all fish collected from the Cobb Seamount were more than six years old, while 85.7% of fish collected from the nearshore samples were more than six years old (Fig. 1). This difference in age composition cannot be explained by differences in gear type because the same gear and mesh size was used in both areas. There are several potential explanations for these differences including differences in fishing pressure, differences in fishing behavior, differences in discard practices, and actual differences in the population age composition.

The argument for differences in fishing pressure relies on the belief that widow rockfish on the Cobb Seamount were heavily exploited prior to 1985 and therefore their population was reduced to very low levels. This argument is supported by Sasaki (1986) who reported that the seamount had, in fact, been heavily fished. Widow rockfish were never specifically mentioned as having been caught by any fishery prior to 1991. While intense fishing pressure on the Cobb Seamount may be responsible for the absence of older widow rockfish, there are arguments against this explanation. First, a sample of 50 harlequin rockfish (*S. variegatus*) had a mean age of 15 years, much older than would be expected if they had experienced similar fishing mortality to the widow rockfish. In addition, even if the Cobb Seamount had experienced extremely heavy fishing pressure, it seems unlikely that virtually all the older fish would have been caught.

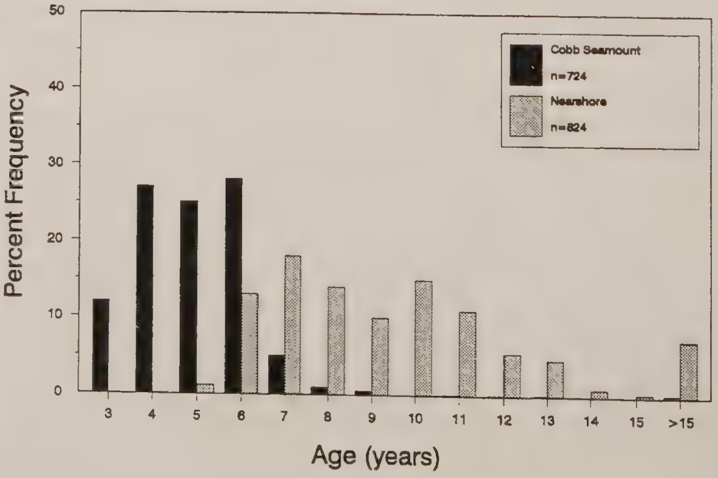

**Figure 1**
Comparison of age composition from widow rockfish caught on Cobb Seamount and the coastal area of northern Oregon.

The argument for differences in fishing behavior has some merit. Fishermen report that the terrain on the Cobb Seamount is very rugged and it is possible that the fishermen tend to keep their nets higher off the bottom to avoid snags than they would in the nearshore areas. This could result in a different age composition if young fish tended to disperse higher into the water column than older fish.

The argument for the difference in age composition being due to a difference in discard practices also has some merit. Fishermen operating under trip limits in the nearshore areas, and having to deal with market demands for larger fish, would tend to discard smaller fish. The problem with this argument is that it would tend to explain a higher proportion of small fish in the Cobb Seamount widow rockfish landings, but it would not explain the virtual absence of older, larger fish which certainly would be retained by the fishermen.

The possibility that the age composition of the two areas is actually different also has merit. It is not known whether the population of widow rockfish on the Cobb Seamount is self sustaining or if the fish recruit to the seamount from the nearshore population. Juvenile rockfish have an extended pelagic phase. During this stage they can be advected offshore. Recent studies of juvenile rockfish off the central California coast have found juvenile rockfish more than 200 miles offshore[1]. If this also occurs off Oregon, then it is possible that some fraction of the existing population on the Cobb Seamount originated as juveniles or larvae, or both, in the nearshore area. While it cannot be completely discounted that adults migrate to the seamount it seems unlikely because adult widow rockfish are not considered pelagic and the seamount is more than 200 miles from the nearest suitable habitat. It is possible that older fish either emigrate from the seamount or experience high mortality for some unknown reason. It is also possible that there was a massive kill of widow rockfish on the Cobb Seamount prior to 1985. Another possibility is that there never were widow rockfish on the Cobb Seamount prior to 1985. This latter possibility may have some merit since yellowtail rockfish appear to be totally absent from the Cobb Seamount; yet, they are quite abundant in the nearshore area, although the habitat at the Cobb Seamount would seem to be ideal for them. If getting to the Cobb Seamount is a fortuitous event, then it is possible that yellowtail rockfish just have not been lucky yet and that widow rockfish have only been lucky recently. Only further studies can determine the cause for the apparent differences in age composition between the Cobb Seamount and the nearshore populations.

Otoliths from many species can undergo a process of vaterite replacement (Gauldie, 1986) in which the aragonite in the otoliths is replaced by vaterite. This process results in a quite distinctive otolith morphology (Fig. 2) and has been observed by the authors in many species of rockfish, flatfish, and other groundfish species. Vateritic otoliths are sometimes called "resorbed" or "crystallized" owing to their somewhat crystalline appearance. In nearshore widow rockfish sampled in Oregon from 1991, only 2.5% of the fish had vateritic otoliths. In contrast, 28 percent of otoliths from Cobb Seamount widow rockfish are vateritic. Gauldie (1986), working with salmon, suggested that vaterite replacement is under single locus genetic control but can be overridden by temperature extremes. It is possible that Cobb Seamount could be subject to temperature extremes during certain oceanographic events like El Niños.

Three other interesting observations have been made about rockfish from Cobb Seamount during this fishery. Rosy rockfish (*S. rosaceous*) was caught; thus a northern range extension for this species was created.[2] Harlequin rockfish have been caught; thus, their southern range has been extended from its previously reported southern limit of Queen Charlotte Sound, British Columbia (Eschmeyer et al., 1983). Five shortbelly rockfish (*S. jordani*) were caught, three of them in excess of 34-cm fork length, which exceeds the largest fish previously known to the authors (33 cm). Studies on other seamounts in the Pacific have shown that rare species, exceptionally large specimens, and range extensions occur on other seamounts (Hughes, 1981).

The Cobb Seamount undoubtedly holds many other surprises for fisheries biologists. Studies of rockfish communities on the Cobb Seamount and how colonization occurs could lead to a better understanding of the population dynamics of this large, valuable group of groundfish. One possible way colonization could occur would be if it were found that strong cohorts on the Cobb Seamount were weak cohorts in the nearshore area and vice versa. This would suggest the possibility that advection of juveniles has an important role in determination of cohort strength which would have major ramifications in management of nearshore fisheries. Continued examination of fish with vateritic otoliths could yield new information, particularly if other populations of fish are found to have a high percentage of vateritic otoliths. Remotely operated vehicle studies would be a useful approach to examine the benthic community to determine its similarity to nearshore areas.

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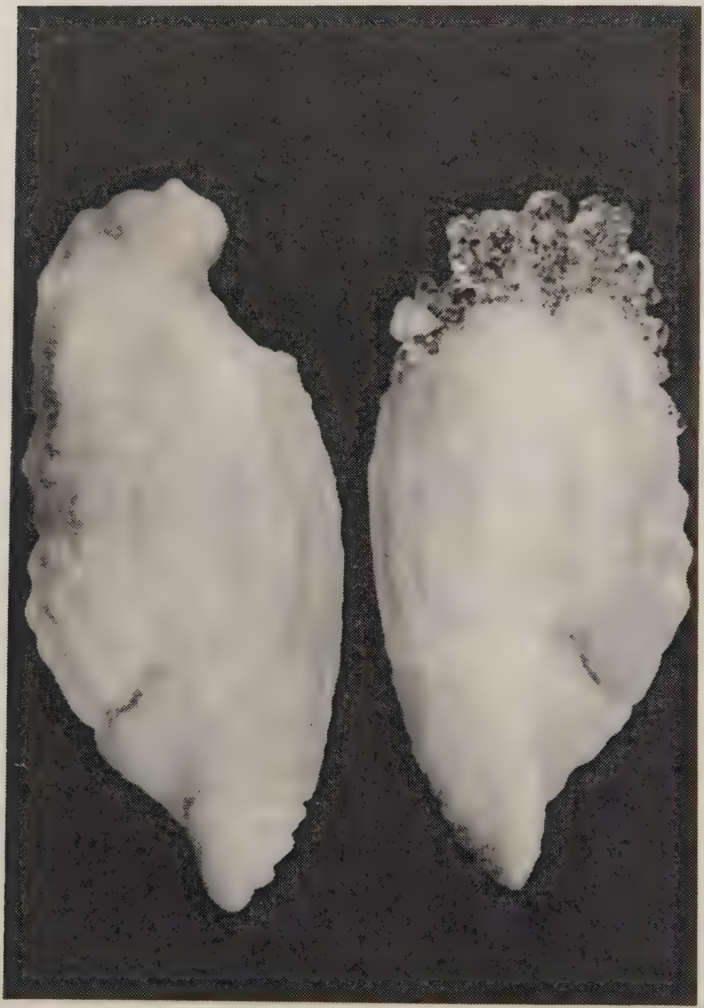

**Figure 2**
Two sagittal otoliths from a widow rockfish. Otolith on the left is normal, while the otolith on the right exhibits the phenomenon known as vaterite replacement.

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# Composition of the 1991 Incidental Kill of Small Cetaceans in the Eastern Tropical Pacific US Tuna Fishery and Two California Gillnet Fisheries

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## ABSTRACT

Data are presented for the observed incidental kill of small cetaceans on 40 US tuna purse-seine vessel-trips and 794 California gillnet vessel-trips. This is the first complete year (1991) that data were collected by observers for California gillnet fisheries. There were 1,002 cetaceans killed incidentally in the US tuna fishery and 69 cetaceans killed incidentally in the California gillnet fisheries sampled. The observed incidental kills are summarized and reported here by geographic area, species, stock and sex. Where life history data were collected, the summary also includes a length distribution for each species and sex, as well as the reproductive condition for the females collected.

KEYWORDS: EASTERN TROPICAL PACIFIC; NORTH PACIFIC; SPOTTED DOLPHIN; SPINNER DOLPHIN; COMMON DOLPHIN; RIGHT WHALE DOLPHIN; WHITE-SIDED DOLPHIN; DALLS PORPOISE; FISHERIES; INCIDENTAL CAPTURE; MORTALITY; GROWTH/LENGTH DISTRIBUTION.

## INTRODUCTION

The National Marine Fisheries Service (NMFS) places biological technicians (observers) aboard US tuna purse-seine vessels and California gillnet vessels to monitor the incidental kill of marine mammals and other protected marine vertebrates. These monitoring programs provide estimates of mortality and reproductive rates which are used to assess the effects of the fisheries on populations of small cetaceans and pinnipeds. The purpose of this report is to document the observed incidental mortality of small cetaceans and the collection of life history data subsampled from the kill by US-registered tuna purse-seine vessels and California gillnet vessels between 1 January and 31 December 1991.

### US tuna fishery

The NMFS has monitored the incidental kill of small cetaceans by the US tuna purse-seine fishery in the eastern tropical Pacific (ETP) since 1968 with the Inter-American Tropical Tuna Commission (IATTC) beginning a complementary program for the international fleet in 1979. Since 1989, the aim has been for complete coverage of the US fleet by fisheries observers. Prior to 1989, 30% observer coverage of the fleet was targeted (Lo *et al.*, 1982). The species most frequently killed as a result of tuna purse-seine fishing operations are the pantropical spotted dolphin (*Stenella attenuata*), spinner dolphin (*S. longirostris*) and common dolphin (*Delphinus delphis*). Several other species of small cetaceans are also killed in relatively low numbers. The composition of the US kill of small cetaceans has been documented since 1979 in a series of reports (Perrin and Oliver, 1982; Oliver *et al.*, 1983; Wahlen *et al.*, 1986; 1987; 1988; Chivers *et al.*, 1989; 1990; Hohn *et al.*, 1991; Peltier *et al.*, 1992), and the non-US kill has also been documented since 1979 by the IATTC (Hammond and Hall, 1985; Hall and Boyer, 1986; 1987; 1988; 1989; 1990; 1992).

### California gillnet fisheries

In July 1990, the NMFS in conjunction with the California Department of Fish and Game (CDFG), initiated a three year program to assess mortality and collect life history data from all species that are killed incidentally in two of the gillnet fisheries operating off the coast of California. The targeted observer coverage for these fisheries is 20% of all vessels trips (Lennert *et al.*, 1993). The two California gillnet (CAGN) fisheries sampled are the set-net fishery targeted for halibut (*Paralichthys californicus*) and Pacific angel shark (*Squatina californica*), and the drift-net fishery targeted for common thresher shark (*Alopias vulpinus*), short-finned mako shark (*Isurus paucus*) and swordfish (*Xiphias gladius*) (Herrick and Hanan, 1988). The non-target species observed killed in the two CAGN fisheries include cetaceans, pinnipeds [California sea lions (*Zalophus californianus*), harbor seals (*Phoca vitulina*), elephant seals (*Mirounga angustirostris*)], sea otters (*Enhydra lutris*) and several species of seabirds and turtles. The species of cetacean most frequently killed is the common dolphin. Mortality observed in this fishery has been reported by several authors (Diamond and Hanan, 1986; Hanan *et al.*, 1986; 1987; 1988; Herrick and Hanan, 1988; Hanan and Diamond, 1989; Perkins *et al.*, 1992a; b; Barlow *et al.*, 1993; Lennert *et al.*, 1993). This report summarizes only the observed incidental kill of small cetaceans.

## METHODS

### US tuna fishery

Data are collected by NMFS and IATTC observers aboard US-registered tuna purse-seine vessels in the ETP. For each set made, the observers record the species, stock and sex of cetaceans involved along with the geographic location of the school and a tally of individual animals killed. Life history data (e.g. specimen length and reproductive condition) are collected from those animals that are brought aboard with the tuna and, therefore, represent a subset of the incidental kill that is tallied.

Procedures for the collection of life history data have been described by Perrin *et al.* (1976). While the procedures for collecting the life history data have not changed, additional materials are now collected (i.e. adrenal glands and biopsy sample). An example of the most recent life history form can be found in Hohn *et al.* (1991), and the data elements are described in Oliver (1991).

Life history and tally data are summarized for all vessel trips between 1 January and 31 December 1991. The number of cetaceans observed killed are summed by 5° block for each species, stock and sex to show the geographic distribution of observed sets (for a complete map of blocks for the ETP, see Perrin and Oliver, 1982). The life history data collected are presented as length frequency distributions for each species and sex, and for females, the life history data are further summarized by reproductive condition (e.g. whether sexually mature, pregnant or lactating). Tally and life history data are also stratified by stock for the pantropical spotted dolphin (northern and southern) and for the spinner dolphin (eastern and whitebelly) (Perrin *et al.*, 1985). We have combined the northern and southern stocks of whitebelly spinner dolphins in accordance with the most recent spinner dolphin stock descriptions given in Perrin *et al.* (1991).

### California gillnet fisheries

NMFS biological technicians are placed on selected California drift- and set-net vessels (Perkins *et al.*, 1992b; Lennert *et al.*, 1993). The observers tally the number and species of cetaceans observed entangled in the nets by geographic location, and life history data are collected from the animals when possible. The procedures for collecting life history data are essentially the same as for the ETP cetacean species, although a few modifications were made to the life history form (Hohn *et al.*, 1991) for the collection of data for pinnipeds (Winchell, 1990). Modifications to the data form include the addition of fields to note whether the total body length measurement was curvilinear, to record flipper length and to note if a skin sample was collected. Because animals cannot always be brought aboard the vessels, the definition of life history data collection also includes cases where only geographic location, species and a skin sample are collected. Otherwise, geographic location, species, sex and length constitute the collection of baseline life history data, as is the case for the ETP observer program.

We have summarized the tally and life history data for small cetaceans collected from all observed vessel–trips made by observers between 1 January and 31 December 1991. The life history data are presented as length frequency distributions for each cetacean species by sex, also presented are data collected on the reproductive condition of females.

## RESULTS

### US tuna fishery

For the third consecutive year, there was 100% observer coverage on all US tuna purse-seine vessels with fishing permits. There was a total of 40 tuna purse-seine trips reported and observed in the ETP during 1991, 16 of which (40%), reported cetacean kill. The observed incidental kill of 1,002 small cetaceans was composed of 634 pantropical spotted dolphins, 271 spinner dolphins, 93 common dolphins and 4 dolphins unidentified to species.

Fig. 1 shows the geographic distribution of purse-seine sets with observed kill. The totals for each 5° square block are summed by species, stock and sex (Table 1). Life history data were collected from 263 of the animals killed on 11 of the 16 trips with observed cetacean kill. These data included total body length measurement for 149 females and 114 males (Table 2) and reproductive condition for 106 of the females (Table 3).

### California gillnet fisheries

In 1991, there were an estimated 4,752 days fished in the drift-net fishery and 7,089 days fished in the set-net fishery. There were 88 drift-net trips accounting for 470 days of fishing observed during the year, and 706 set-net trips were observed, which corresponds to the same number of fishing days. In both fisheries, the observer coverage accounted for 10% of the total number of fishing days reported. Cetaceans were incidentally killed on 34 of the 88 observed drift-net trips and on only four of the 706 observed set-net trips. A total of 64 cetaceans were observed killed on drift-net trips: 44 common dolphins, 7 northern right-whale dolphins (*Lissodelphis borealis*), 5 Pacific white-sided dolphins (*Lagenorhyncus obliquidens*), 5 Risso's dolphins (*Grampus griseus*), 2 Dall's porpoise (*Phocoenoides dalli*) and one unidentified cetacean. In the set-net fishery, five harbor porpoise (*Phocoena phocoena*) were observed killed. In the drift-net fishery, 34 of the 35 trips observed that reported cetacean kill also collected life history data. Life history data were collected from one harbour porpoise on a set-net trip. We have plotted (Fig. 2) the geographic positions of sets in which cetaceans were observed killed but no life history data were collected and those sets with life history data collected for the two fisheries observed. Life history data were collected from 54 of the 69 animals observed killed in both fisheries, including a measure of total body length for 17 females and 26 males (Table 2), reproductive condition for 14 of the females (Table 3) and skin samples for 12 specimens (5 females, 5 males, and 2 of unknown sex).

## DISCUSSION

### US tuna fishery

The observed incidental kill during 1991 is down markedly from the two preceding years that also had 100% observer coverage. The observed incidental kill of 1,002 cetaceans in 1991 compares to a kill of 12,548 and 5,083 cetaceans for 1989 and 1990, respectively (Hohn *et al.*, 1991; Peltier *et al.*, 1992). Correspondingly, the total number of trips and the number of trips with observed kill were also down markedly in 1991. Only 40% of all observed trips ($n = 40$) reported cetacean kill in 1991, whereas 88% of the trips ($n = 123$) in 1989 reported kill, and in 1990, 64% of the trips ($n = 107$) reported kill. The decline in the incidental kill of small cetaceans in the ETP may be attributed to the reduction of the US tuna purse-seine fleet that followed the US tuna canneries' decision in April 1990 to not buy tuna caught in conjunction with dolphins. Currently, only seven tuna purse-seine vessels remain in the US fleet; a reduction from 31 vessels in 1989 and 17 vessels in 1990 (R. Rasmussen, SWFSC, pers. comm.).

The life history data collected in 1991 account for 26% of the total observed kill and compares to average collection rates for the periods 1979–80 and 1981–87, of 43% and 20%, respectively. The collection rates for life history data in 1991 are not statistically different (chi-square, $\alpha = 0.05$) from those for 1989 (24%) and 1990 (26%) when observer coverage was also 100%. The fraction of the kill collected

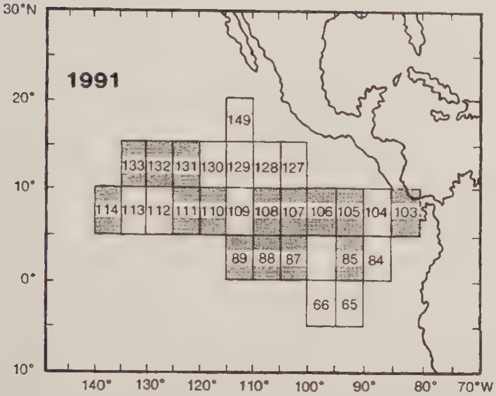

Fig. 1. Geographic distribution of the observed incidental kill of small cetaceans in the ETP for 40 trips by US-registered vessels during 1991. The data are summarized by 5° square areas. The stippled blocks indicate areas where both a tally of the observed kill and life history data were collected; numbered blocks without shading are regions where only tally data were collected.

with life history data complete with reproductive information for females is 11%, significantly more than was collected in 1989 and 1990 (chi square, $p<0.005$). In 1989, 7% of the life history data collected included reproductive data, and in 1990, 8% of the sample was represented by reproductive data (Chivers *et al.*, 1990; Hohn *et al.*, 1991; Peltier *et al.*, 1992). This compares to an average longterm collection rate of 12% and 6% for the periods 1979–80 and 1981–87, respectively. The data show that 51% of the cetaceans collected were sexually immature, with 69% of the common dolphins that had reproductive data collected having the highest percentage. This is a higher proportion, but not significantly different (chi square, $\alpha=0.05$) than in recent years (43% and 42% for 1989 and 1990, respectively).

### California gillnet fisheries

This report documents the data collected during the first complete calendar year in which the CAGN observer program was operating. During 1991, 69 cetaceans were reported killed compared to 19 cetaceans during the first six months of the program, July-December 1990 (Lennert *et al.*, 1993). Cetacean kill was reported on 40% of the observed drift-net trips, while less than 1% of the set-net trips reported cetacean kill. Although observer coverage is targeted for 20% of days fished, only 10% were observed in 1991. This is more than were observed between July and December 1990 when observer coverage of the fisheries was 4% for the drift-net fishery and 5% for the set-net fishery (Lennert *et al.*, 1993).

Life history data collected from these fisheries accounted for 78% of the observed cetacean kill, with 20% of the observed kill including data on reproductive condition for females. Because of small sample sizes, we are not yet able to estimate population parameters for the species incidentally killed in the fisheries, but 71% of all the cetaceans with reproductive data collected were sexually mature.

Table 1

Total observed kill of dolphins from the ETP by geographic location (5° square block) and sex. Pantropical spotted dolphins (*Stenella attenuta*) and spinner dolphins (*S. longirostris*) are separated by stock. The total for each stock includes dolphins of unknown sex. Four dolphins unidentified to species were not included in the table. All were of unknown sex. No kill was reported for coastal spotted or Costa Rican spinner dolphins.

| 5° block | Northern offshore spotted | | | Southern offshore spotted | | | Eastern spinner | | | Whitebelly spinner | | | Common | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M | F | Total | M | F | Total | M | F | Total | M | F | Total | M | F | Total |
| 65 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| 66 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 84 | 3 | 3 | 24 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 85 | 19 | 11 | 53 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 |
| 87 | 3 | 1 | 32 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 88 | 7 | 2 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 41 | 0 | 0 | 0 |
| 89 | 5 | 4 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 103 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 16 | 14 | 55 |
| 104 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 6 |
| 105 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 10 | 20 | 32 |
| 106 | 1 | 11 | 35 | 0 | 0 | 0 | 6 | 3 | 9 | 0 | 0 | 8 | 0 | 0 | 0 |
| 107 | 8 | 10 | 58 | 0 | 0 | 0 | 4 | 6 | 17 | 1 | 0 | 5 | 0 | 0 | 0 |
| 108 | 29 | 38 | 108 | 0 | 0 | 0 | 3 | 8 | 17 | 26 | 21 | 63 | 0 | 0 | 0 |
| 109 | 2 | 6 | 8 | 0 | 0 | 0 | 0 | 2 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| 110 | 16 | 34 | 84 | 0 | 0 | 0 | 4 | 0 | 4 | 6 | 15 | 24 | 0 | 0 | 0 |
| 111 | 1 | 3 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 3 | 5 | 0 | 0 | 0 |
| 112 | 5 | 9 | 14 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 3 | 0 | 0 | 0 |
| 113 | 0 | 0 | 43 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 |
| 114 | 1 | 8 | 14 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 6 | 10 | 0 | 0 | 0 |
| 127 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 128 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 |
| 129 | 4 | 2 | 7 | 0 | 0 | 0 | 4 | 3 | 12 | 0 | 0 | 0 | 0 | 0 | 0 |
| 130 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 131 | 22 | 23 | 52 | 0 | 0 | 0 | 9 | 5 | 18 | 0 | 0 | 0 | 0 | 0 | 0 |
| 132 | 3 | 3 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 4 | 9 | 0 | 0 | 0 |
| 133 | 0 | 2 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 7 | 0 | 0 | 0 |
| 149 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total | 130 | 171 | 629 | 0 | 0 | 5 | 30 | 27 | 87 | 49 | 56 | 184 | 26 | 35 | 93 |

Table 2

Length frequencies for all cetaceans with life history collected from the ETP US tuna fishery and two CAGN fisheries.

| | Eastern Tropical Pacific cetaceans | | | | | | | | California Temperate cetaceans | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Northern offshore spotted | | Eastern spinner | | Whitebelly spinner | | Common | | Northern right-whale dolphin | | Pacific white-sided | | Common | | Dall's porpoise | |
| Length(cm) | M | F | M | F | M | F | M | F | M | F | M | F | M | F | M | F |
| 0- 74 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 75- 79 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 80- 84 | 0 | 0 | 0 | 0 | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 85- 89 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 90- 94 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 95- 99 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 100-104 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 105-109 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 110-114 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 115-119 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| 120-124 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 125-129 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 130-134 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 135-139 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 140-144 | 1 | 4 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 145-149 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 150-154 | 3 | 3 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| 155-159 | 2 | 6 | 1 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 160-164 | 7 | 4 | 2 | 0 | 2 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 165-169 | 7 | 9 | 0 | 2 | 1 | 5 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| 170-174 | 5 | 8 | 1 | 0 | 4 | 6 | 0 | 4 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 |
| 175-179 | 5 | 6 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 0 |
| 180-184 | 6 | 8 | 1 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 1 | 0 | 2 | 2 | 0 | 0 |
| 185-189 | 4 | 16 | 2 | 0 | 1 | 0 | 5 | 1 | 0 | 0 | 1 | 0 | 4 | 2 | 0 | 0 |
| 190-194 | 4 | 11 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| 195-199 | 6 | 5 | 0 | 0 | 0 | 0 | 2 | 5 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 |
| 200-204 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| 205-209 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| 210-214 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 215-219 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| 220-224 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 225- | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total | 65 | 90 | 12 | 5 | 19 | 31 | 18 | 23 | 0 | 4 | 2 | 3 | 23 | 10 | 1 | 0 |

Table 3

Reproductive condition of female cetaceans with life history collected from the ETP US tuna fishery and two CAGN fisheries. Percentages include females without reproductive information available. 'Maturity undetermined' indicates that only minimum life history data were collected.

| | Eastern Tropical Pacific cetaceans | | | | | | | | California Temperate cetaceans | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Northern offshore spotted | | Eastern spinner | | Whitebelly spinner | | Common | | Northern right-whale dolphin | | Pacific white-sided | | Common | |
| Reproductive condition | N | % | N | % | N | % | N | % | N | % | N | % | N | % |
| Maturity undetermined | 29 | 32.2 | 1 | 20.0 | 13 | 41.9 | 0 | 0.0 | 1 | 20.0 | 0 | 0.0 | 5 | 41.7 |
| Sexually immature | 28 | 31.1 | 2 | 40.0 | 8 | 25.8 | 16 | 69.6 | 0 | 0.0 | 1 | 33.3 | 3 | 25.0 |
| Sexually mature: | | | | | | | | | | | | | | |
| Condition undetermined | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 1 | 4.3 | 0 | 0.0 | 0 | 0.0 | 2 | 16.7 |
| Pregnant only | 6 | 6.7 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 2 | 66.7 | 0 | 0.0 |
| Pregnant and lactating | 7 | 7.8 | 0 | 0.0 | 0 | 0.0 | 2 | 8.7 | 0 | 0.0 | 0 | 0.0 | 1 | 8.3 |
| Lactating only | 11 | 12.2 | 1 | 20.0 | 6 | 19.4 | 2 | 8.7 | 1 | 20.0 | 0 | 0.0 | 0 | 0.0 |
| Resting with a corpus luteum | 2 | 2.2 | 1 | 20.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| Resting without a corpus luteum | 6 | 6.7 | 0 | 0.0 | 3 | 9.7 | 2 | 8.7 | 3 | 60.0 | 0 | 0.0 | 1 | 8.3 |
| Post reproductive | 1 | 1.1 | 0 | 0.0 | 1 | 3.2 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| Total | 90 | 100.0 | 5 | 100.0 | 31 | 100.0 | 23 | 100.0 | 5 | 100.0 | 3 | 100.0 | 12 | 100.0 |

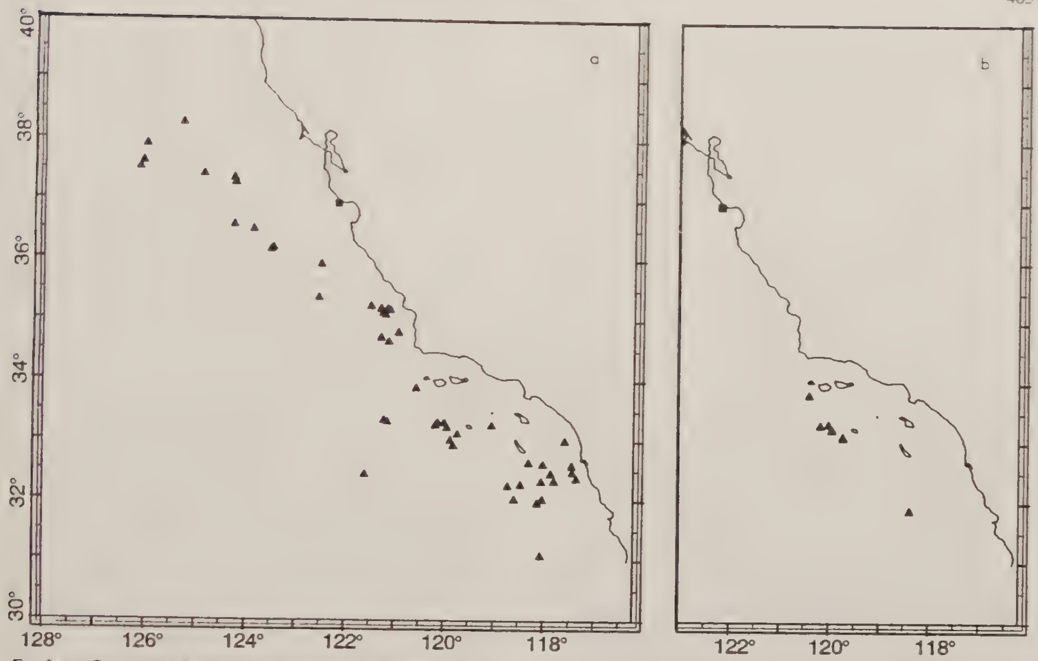

Fig. 2. (a) Geographic distribution of sets having incidental kill of cetaceans for which tally and life history data were collected in the drift-net fishery. Each square represents at least one cetacean but no more than three. No life history data were collected on set-net trips. (b) Geographic distribution of the tally of the observed incidental kill of small cetaceans from the two CAGN fisheries for which no life history data were collected. Each symbol represents one net-set with a maximum of three animals observed killed per symbol. The squares represent tally from the drift-net fishery and the triangles represent tally from the set-net fishery.

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# ROSTRAL FUSION AS A CRITERION OF CRANIAL MATURITY IN THE COMMON DOLPHIN, *DELPHINUS DELPHIS*

When examining sexual dimorphism, individual variation, or geographical variation in cranial characters in a mammal, it is necessary to decide which skulls in a series to include in the analysis as adults. For dolphins of the genus *Stenella,* distal fusion of the premaxillae with the maxillae was proposed as a criterion of cranial adulthood by Dailey and Perrin (1973); this was based on the observation by Perrin (1972, 1975) that such fusion occurred at about the age (based on *growth layer groups* in the dentine, *sensu* Perrin and Myrick, 1981) at which elongation of the rostrum ceased in series of pantropical spotted dolphins, *S. attenuata,* and spinner dolphins, *S. longirostris.*

We recently examined a large series of skulls of short-beaked common dolphins, *Delphinus delphis,* thought to have come from a single interbreeding population (Heyning and Perrin, in press), and found that distal fusion is not an accurate marker of cranial maturity in this species. The rostrum on average continues to elongate, at least in males, until slightly after distal fusion begins. This is apparent in comparison of length-frequency distributions of rostrum length (measured from a line across the bases of the antorbital notches) for specimens known to be physically mature (all vertebral epiphyses fused to centra; A in Fig. 1) and for specimens physically immature but with rostral fusion (B in Fig. 1); the difference between means for males is statistically significant at $0.10 > P > 0.05$ (95% confidence intervals 235.3–250.9 cm and 249.4–258.8 cm for B and A, respectively, in Fig. 1).

We found that combined criteria of distal rostral fusion and sexual maturity (presence of lactation, fetus, or at least one ovarian corpus in female; testis weight $\geq 100$ g in male; hatched portions of B in Fig. 1) yielded rostrum-length frequencies in physically immature specimens more in line with those in physically mature specimens, although the sample sizes were relatively small.

These results suggest that male adult series of common dolphins used for analyses of non-developmental variation should include only skulls of specimens known to be physically mature and perhaps those known to both exhibit distal fusion and be sexually mature. In view of the small sample sizes in the present analysis, it would seem prudent to do the same for females. If ages have been determined for a large series of specimens, other specimens known to be of an age at which physical maturity is universal can also be included.

These cautions imply that series for analyses of adult variation in this species, and possibly others, should not include "beach pick-up" skulls for which information on postcranial skeleton or on sexual maturity is not available and for which age cannot be estimated relatively precisely.

The results accord with those of Mead and Potter (1990) for *Tursiops truncatus*; they found that distal fusion ("skull maturity" in their paper) occurs in

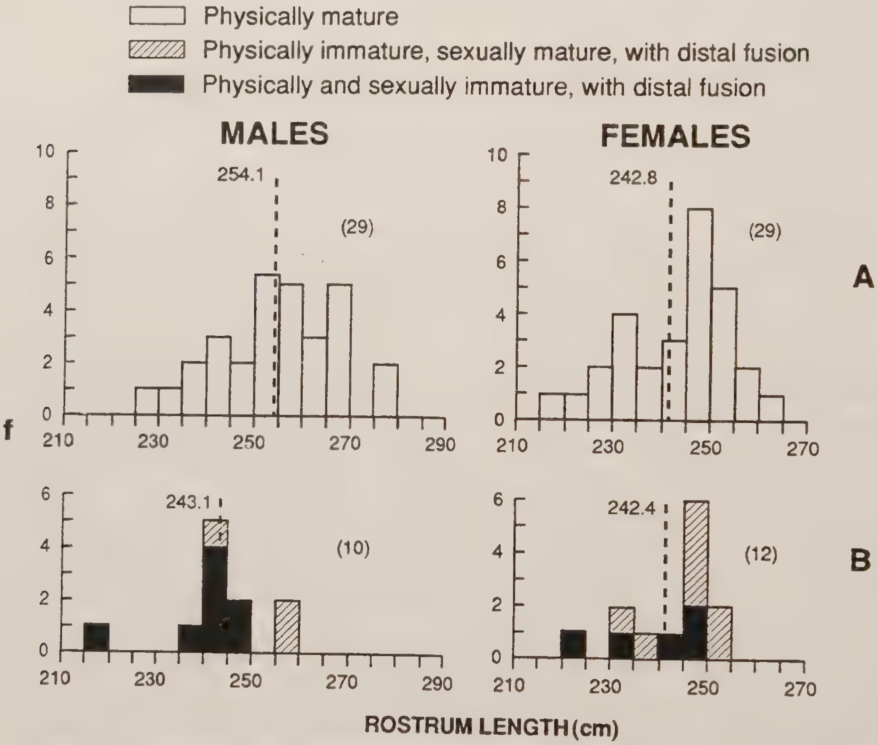

*Figure 1.* Frequency distributions of rostrum length and average rostrum length (dashed lines) in physically mature (upper) and physically immature (lower) male (left) and female (right) specimens of *Delphinus delphis.*

that species on average at least several years (approximately 7 growth layer groups) before attainment of sexual maturity. However, they did not state whether the skull continues to grow after the onset of distal fusion.

Perrin's original (1972, 1975) conclusions about the apparent correlation of cranial maturity and distal fusion in both males and females in *Stenella* spp. were based on relatively small series of adult specimens for which age had been estimated from tooth sections. The results reported here for *Delphinus delphis* indicate that the question should be re-examined based on larger series.

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# IDENTIFICATION OF GEOGRAPHIC FORMS OF COMMON DOLPHIN (*Delphinus delphis*) FROM AERIAL PHOTOGRAMMETRY

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## ABSTRACT

At least four morphologically distinct forms of common dolphins are found in the eastern Pacific. We compared length data for common dolphins photographed from the northern, central and southern regions as defined by Perrin *et al.* (1985) and found significant differences in average length for adult animals (>150 cm) and for "adult females" defined for our purposes as animals accompanied by calves. Analyses of calculated birth dates for calves demonstrated differences in timing of reproduction between the geographically adjacent forms. Length distributions from aerial photographs and samples collected from the purse seine fishery were strikingly similar. This work demonstrates a new, noninvasive method for obtaining unbiased life history and morphological data.

Key words: common dolphin, *Delphinus delphis,* geographic forms, length, timing of reproduction, aerial photography, photogrammetry.

Determining the intraspecific structure of the widely distributed and geographically varied common dolphin, *Delphinus delphis,* has been problematic. In fact, over two dozen nominal species have been proposed although currently most authorities recognize one highly varied species (Heyning and Perrin 1991). Evans (1975, 1982) examined the morphology and distribution of this species in the eastern Pacific and described five distinct forms: (1) a short-beaked form off southern California; (2) a short-beaked form off Baja California; (3) a large, long-beaked neritic form north of 20°N; (4) a short-beaked central tropical form; and (5) a southern short-beaked form. He also suggested the possibility of an "equatorial-oceanic" population. Based on more sightings and a larger sample of aged specimens, Perrin *et al.* (1985) combined the southern California and Baja short-beaked populations and expanded the range of the southern form to include Evan's equatorial-oceanic group (Fig. 1). They defined a southern stock based on a hiatus of sightings between the central and southern populations.

Most specimens used in the reports cited above were killed incidental to purse seine fishing for yellowfin tuna (Perrin 1969). The use of fishery samples to obtain data on life history and morphology usually raises questions concerning

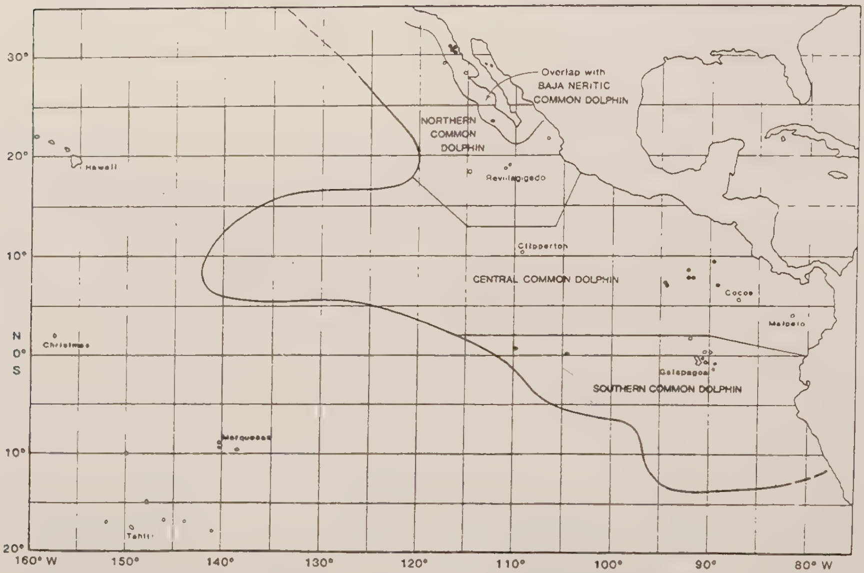
30°
20°
10°
N
0°
S
10°
20°
160° W
150°
140°
130°
120°
110°
100°
90°
80° W
Overlap with BAJA NERITIC COMMON DOLPHIN
NORTHERN COMMON DOLPHIN
Hawaii
Revillagigedo
Clipperton
CENTRAL COMMON DOLPHIN
Cocos
Malpelo
Christmas
Galapagos
SOUTHERN COMMON DOLPHIN
Marquesas
Tahiti

*Figure 1.* Recommended management units for *Delphinus delphis* from Perrin et al. 1985. Locations of schools used in this report are indicated by dark circles.

potential bias in the sample (*e.g.,* Perrin and Reilly 1984). For example, the vulnerability of dolphins to fishing mortality may vary with age, sex, or reproductive condition. If so, then samples obtained from the fishery are biased, and the validity of studies using these samples are in question. In addition, the geographic distribution of specimens collected from the fishery is restricted to areas where common dolphin and tuna associate.

In this study we avoid the above-mentioned biases by using low-level aerial photogrammetry to examine the geographic forms of free-ranging common dolphins. Length distributions of common dolphins from the northern, central, and southern regions (Fig. 1) were compared. We also compared lengths of adult animals swimming with calves, defined as "adult females," among these regions and examined calculated birth dates of calves for evidence of reproductive seasonality. Similar techniques have been applied to the study of large cetaceans (Scott and Winn 1980; Whitehead and Payne 1976; Cubbage and Calambokidis 1987; Sumich 1984, 1986; Koski *et al.* 1992; Withrow and Angliss 1992), but this is the only large scale application of aerial photogrammetric sampling to the study of geographic concordance of intraspecific differences in small cetaceans (Scott and Perryman 1991).

## METHODS

*Photographic sampling*—Aerial photographs of 14 schools of common dolphins were used for this report (Table 1). We took the photographs from a Hughes 500D helicopter that was deployed from the NOAA Ship *David Starr*

*Table 1.* Schools of common dolphins used in length comparison study. School size determined by observer estimates or counts from photographs.

| Flight date | School position | Estimated school size | Number measured |
|---|---|---|---|
| 9/14/88 | 00°41′N; 109°59′W | 155 | 10 |
| 9/17/88 | 00°02′N; 104°25′W | 1,840 | 40 |
| 10/10/88 | 07°05′N; 089°08′W | 870 | 25 |
| 10/16/88 | 08°49′N; 092°08′W | 649 | 57 |
| 12/1/88 | 23°25′N; 112°19′W | 343 | 72 |
| 10/19/89 | 07°56′N; 091°55′W | 226 | 68 |
| 10/19/89 | 07°54′N; 092°02′W | 167 | 57 |
| 11/15/89 | 07°04′N; 094°16′W | 30 | 9 |
| 11/15/89 | 07°03′N; 094°16′W | 377 | 37 |
| 10/15/90 | 09°35′N; 089°36′W | 125 | 85 |
| 12/5/90 | 30°10′N; 116°16′W | 562 | 171 |
| 12/5/90 | 30°16′N; 116°12′W | 1,175 | 393 |
| 12/5/90 | 30°31′N; 116°15′W | 600 | 43 |
| 12/5/90 | 30°47′N; 116°22′W | 1,100 | 274 |

*Jordan*. This sampling was part of a research program conducted by the National Marine Fisheries Service to monitor trends in size of dolphin stocks that are killed incidental to purse seine fishing for yellowfin tuna (Holt and Sexton 1989).

The photographs were taken with a KA45A military reconnaissance camera that was mounted vertically below the fuselage of the helicopter. The camera was designed to collect high resolution, medium format (127 mm) images from high-speed aircraft flying at low altitudes. It has a medium focal length, fixed focus lens (152 mm), with a maximum aperture of f2.8. The camera's focal plane shutter consists of two metal curtains that sweep a slit of light along the film plane, parallel to the direction of flight. When used from a moving platform, this type of shutter can cause some distortion and blurring of the image due to the relative movement between the camera and the scene. The KA45A counteracts this problem with a forward image motion compensation (FMC) system that moves the film at precisely the same speed and direction as the image while the shutter is open. The speed of film movement is a function of altitude and ground speed. FMC reduces distortion and greatly improves image resolution.

All of the photographs were taken with Kodak Aerial Plus-X black and white film. We exposed the film through a medium yellow filter (Wratten #9) to reduce the amount of blue light reaching the film, thus enhancing the contrast between the dolphins and their blue background. The photographs were taken at altitudes between 200 and 300 meters and at a ground speed of about 113 km/hr. As each frame was exposed, a computer-based data acquisition system automatically logged both the altitude and time. This system also allowed the scientists in the helicopter to record other information for each pass over the school.

*Length determination*—We selected dolphins for measurement that were

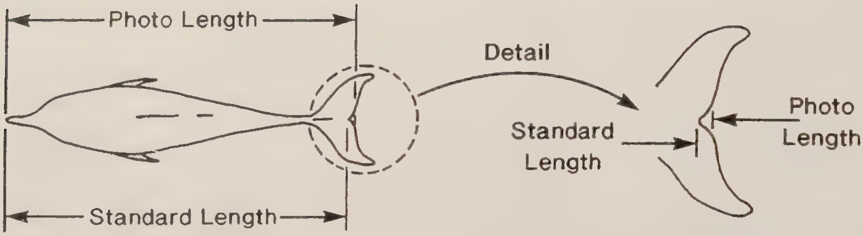

*Figure 2.* Illustration of the difference between standard length and length measured from aerial photographs.

swimming parallel to and very near the surface. Dolphins that were jumping, surfacing, or diving were excluded from the sample. We measured the dolphins from the tip of the rostrum to the trailing edge of the tail flukes (Fig. 2). We selected these points because the fluke notch was very difficult to see in most of the images. For adult specimens this measurement is about 2.5 cm longer than standard length (Norris 1961).

We measured the dolphins on the original negatives with the aid of a stereocomparator, which records distance measurements to the nearest micron. A micron corresponds to roughly 1.5 mm on the ground from our normal sampling altitude of 230 m. These measurements were supplemented and verified with a variable ocular micrometer installed in a stereo zoom microscope.

In vertical photographs the relationship between the size of an object and its image on the film is determined by the ratio of the focal length of the lens and the distance from the camera to the object. This ratio is commonly called the scale of the photograph and is defined as **scale** = **A/f** = **o/i** where **A** = altitude, **f** = lens focal length, **o** = size of object photographed, and **i** = size of the image of the photographed object.

In our study focal length remained constant and the scale of each image was determined by the altitude recorded from the radar altimeter. To calibrate the radar altimeter, we photographed objects of known size (target arrays ashore and the ship at sea) and compared altitude derived from measurements with recorded altitude.

*Measurement precision and accuracy*—There are several potential sources of error in determining the true size of an object from its image on an aerial photograph. In topographical aerial photogrammetry, objects of known size and configuration can be photographed and then measured to determine accuracy of a photographic sampling system. When aerial photogrammetry is applied to the study of marine mammals, known-sized animals are generally unavailable and indirect techniques must be used to estimate the magnitude of the errors inherent in the sampling. In this study we conducted three experiments to examine the accuracy and precision of our data.

To test the effect of varying altitude of photography on the accuracy of our measurements, we photographed three painted dolphin targets from altitudes of 200, 240, and 260 meters, the range of altitudes we used in the field. We painted the dolphins light blue-grey against a darker blue background to simulate the low subject to background contrast we encountered over the tropical Pacific. Measurements of known-sized objects near the targets were used to determine the scale of each image. For each pass the three dolphins were independently measured ten times in sequence by two individuals.

Because measuring targets was probably easier than measuring dolphins swimming under water, we also tested the precision of our length measurements by repeatedly measuring five dolphins from a single photograph. We selected dolphin images of varying quality and of both adults and calves. The test was performed rapidly and at the end of eight hours of measurement in an attempt to add the element of fatigue to the sample.

In addition to errors in measurement of the images, errors in instantaneous readings of altitude, image distortion from tip or tilt of the camera, and the refraction of light as it passes through the water all impact the accuracy of our dolphin length measurements. Also, the flex of the bodies of the dolphins associated with normal swimming movements changes their apparent length when viewed from above. Dolphins that were moderately arched or tilted were easily eliminated from the data set because their rostrums or flukes were not visible from above. However, measurements of animals that were slightly arched or tilted still remain in the data set and our estimates of the true length of these dolphins are likely negatively biased.

To determine the variability in the measurements associated with all these sources of error, we examined the data for dolphins that were measured in three or four photographs from the same pass. In this exercise and the two described above, we used the coefficient of variation as a measure of the relative precision of the measurements. We also compared a subset of our length sample with published data taken from specimens to determine whether the biases associated with the different sampling regimes produced different results.

*Data analysis*—Our photographs included schools from each of the three management units recommended by Perrin *et al.* (1985; Fig. 1). In the northern region, a short-beaked and a much larger long-beaked form occur sympatrically but apparently do not school together (Evans 1975). We examined the length distributions of the schools from this region first to determine the stock mix in this sample. Only data for the short-beaked form were used in comparisons among the three regions.

In Perrin *et al.* (1985) morphological differences between putative stocks of common dolphins were demonstrated by comparing the means of length distributions for mature male and female specimens from the northern and central regions. Obviously, we could not directly examine the sexual characters of the dolphins in our photographs, so we devised two methods for stratifying our length samples for comparison with the strata used by Perrin and his co-workers. These two methods and a technique for detecting reproductive seasonality are described below.

*Method #1–modes*—Our length distributions from each region included a small sample of calves and young animals and a larger sample mode containing subadult and adult age classes (Fig. 3). We eliminated the youngest animals from the samples using length as the limiting criteria (<150 cm) and tested

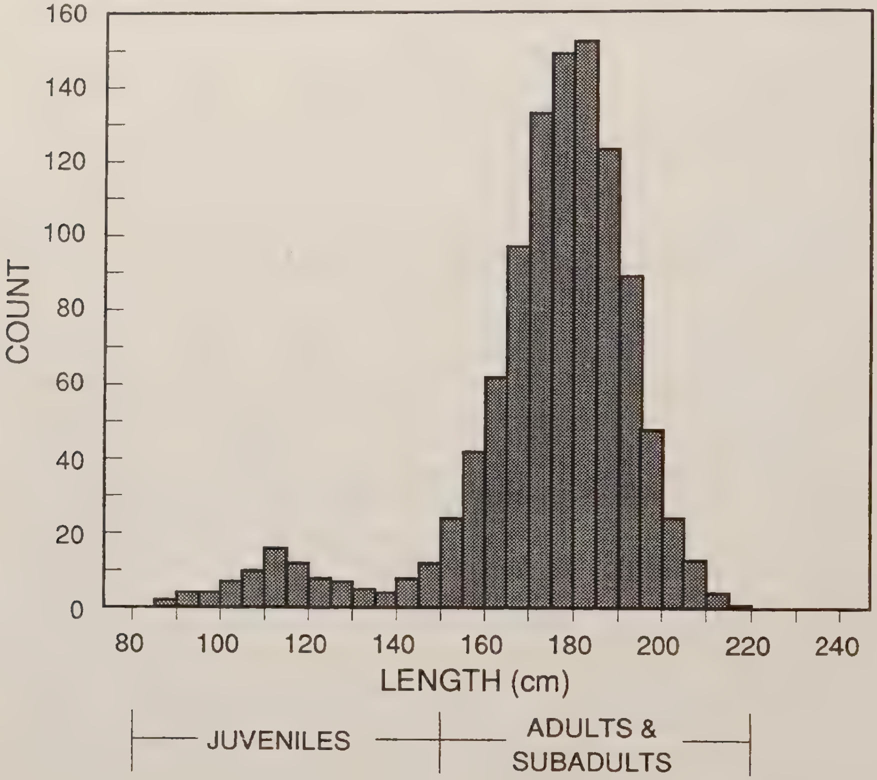

*Figure 3.* Histogram of lengths for common dolphins from the northern region.

for regional differences in size with an ANOVA. We selected the Tukey-Kramer procedure for pair-wise comparison because of its power in tests with unequal sample sizes (Day and Quinn 1989). Because the selection of 150 cm as a minimum size for this sample was somewhat arbitrary, we repeated the analysis with minimum values of 155, 160 and 165 cm.

*Method #2—"adult females"*—The unique association between cows and calves has been noted for a wide range of cetaceans (Norris and Prescott 1961, Taber and Thomas 1982, Wells and Scott 1990, Pryor and Shallenberger 1991), and this behavior has been used to identify cows or adult females in several studies (Whitehead and Payne 1976, Würsig and Würsig 1980, Sumich 1984, Cubbage and Calambokidis 1987, Best 1990, Jones 1990, Scott and Perryman 1991, Miller *et al.* 1992, Koski *et al.* 1993). In our aerial photographs, calves (dolphins <145 cm) were consistently found swimming closely alongside a larger animal (>155 cm). The distance between these cow-calf pairs was about one-fourth that between dolphins of approximately adult size. Based on the consistency of this association in all of our images and the work cited above, we have assumed that the larger animal swimming closely alongside a calf was an adult female. Because this determination was made entirely on behavior, we qualify the term with quotation marks, "adult females," whenever we are referring to a sample of lengths based on the above assumption. We conducted an additional ANOVA as described above to test the hypothesis that "adult females" from the three regions did not differ in length.

*Reproductive seasonality*—Typically, postnatal growth in delphinids is very rapid and almost linear for the first year. During this period when increases in length are large relative to the variability in length at age, seasonal modes in length distributions and frequency histograms of back-projected birth dates have been used to investigate patterns of growth and reproductive seasonality for several stocks of tropical dolphins (Perrin *et al.* 1976, Perrin *et al.* 1977, Barlow 1984, Perrin and Henderson 1984, Hohn and Hammond 1985).

For common dolphins a very limited amount of information is available on growth rates from specimens taken in the eastern Pacific (Hui 1973). In our first analysis of reproductive seasonality, we used estimates of average length at birth for the northern (81.3 cm) and central (79.0 cm) stocks and assumed that length at birth for the southern stock was the same as in the north. We used the estimated length at 1 yr of 135 cm that Hui (1973) reported for common dolphins taken off southern California and Baja California, Mexico as our best estimate of the average length at 1 yr for all three stocks. Assuming linear growth during the first year, we back-projected the birth dates for all dolphins $< 135$ cm in length.

We generated a second distribution of back-projected birth dates using the published lengths at birth (80 cm) and one year (123 cm) for the northern spotted dolphin (Hohn and Hammond 1985). We selected the spotted dolphin as the model for this second data set because of its similarity in size to the common dolphin and the large body of published information on growth for this stock of tropical dolphins.

We used Kuiper's modification of Kolmogorov's test (modified $K$ test) for comparisons of circular distributions (Batschelet 1965) to test the hypothesis that these birth-date distributions were uniform (as done by Barlow 1984). This is a nonparametric test for goodness-of-fit for cumulative distributions. Because critical values for two-tailed tests have not been tabulated, this test was only applied in comparisons of sample distributions with uniform distributions.

All statistical tests not specifically referenced were performed with the program Super ANOVA distributed by Abacus Concepts, Inc., Berkeley, California. Tests were considered significant at $P < 0.05$ unless stated otherwise.

## RESULTS

*Altitude calibration*—We compared calculated altitude ($A_m$) from measurements of known-sized objects with simultaneous readings from our radar altimeter and found a consistent bias in the recorded altitudes ($A_r$). The linear regression equation shown below describes the relationship between $A_m$ and $A_r$.

$$A_m = 1.013A_r - 33.755 \qquad (r^2 = 0.993) \qquad (1)$$

*Table 2.* Lengths for three painted dolphin targets measured independently by two individuals (A and B). Each length is the mean of 10 measurements. True target length is in parentheses.

| Altitude (m) | Dolphin target no. 1 (84.6 cm) | | Dolphin target no. 2 (177.4 cm) | | Dolphin target no. 3 (191.5 cm) | |
|---|---|---|---|---|---|---|
| | A | B | A | B | A | B |
| 200 | 84.9 | 84.4 | 175.7 | 174.3 | 190.7 | 191.3 |
| 240 | 85.1 | 86.1 | 176.6 | 178.7 | 191.1 | 192.1 |
| 260 | 86.3 | 85.7 | 176.3 | 178.0 | 192.8 | 192.8 |

For each school, this formula was used to correct the recorded altitude before the lengths of the dolphins were calculated.

During the 1990 field season the radar altimeter failed and was returned to the manufacturer for repairs. When the instrument was reinstalled, we recalibrated it and found that the relationship between $A_m$ and $A_r$ had changed. The new relationship was

$$A_m = 1.016A_r - 12.211 \qquad (r^2 = 0.992) \tag{2}$$

This relationship was used to correct the recorded altitude during the last two legs of the 1990 survey.

*Accuracy and precision in length determination*—For half of the 18 samples the measurements of the dolphin targets from the aerial photographs were within 1 cm of the true length of the painted dolphin figures (Table 2). The measurements from the lowest altitude were consistently smaller for all targets and interpreters, but the differences between lengths for this range of altitudes were too small to require corrections or a modification in sampling techniques.

Repeated measurements of targets or animals from a single photograph indicate that the errors associated with the measurement process are very small (Table 3). When we compared measurements for the same dolphin in three or four different frames, the mean and range for the coefficients of variation increased but still remained at an acceptably low level. The additional variability in different

*Table 3.* Measurement precision, expressed as coefficients of variation, for replicate measurements of dolphin-shaped targets and of dolphins from single frames, and for measurements of dolphins from 3–4 successive frames.

| Measured object | No. dolphins measured | Measurements per dolphin | Mean of CVs | Range of CVs |
|---|---|---|---|---|
| Dolphin targets individual A | 3 | 30 | 0.008 | 0.005–0.012 |
| Dolphin targets individual B | 3 | 30 | 0.014 | 0.007–0.020 |
| Dolphins in one frame | 5 | 5 | 0.009 | 0.004–0.012 |
| Dolphins in different frames | 54 | 3–4 | 0.026 | 0.001–0.083 |

*Table 4.* Comparison of published length information for adult female common dolphins (Perrin *et al.* 1985, Heyning and Perrin 1991) with lengths of "adult females."

| Data source | Neritic or long-beaked | Northern | Central | Southern |
|---|---|---|---|---|
| Specimen data | | | | |
| *n* | 10 | 82 | 306 | 6 |
| Mean | 207.7 | 178.5 | 194.3 | 188.5 |
| SD | —[a] | 7.30 | 6.80 | 6.86 |
| Range | 193–224 | 155–200 | 170–215 | 180–198 |
| Photographic data | | | | |
| *n* | 5 | 100 | 41 | 20 |
| Mean | 206.2 | 179.2 | 194.8 | 184.3 |
| SD | 13.40 | 8.79 | 8.96 | 6.80 |
| Range | 185–217 | 159–200 | 169–212 | 172–197 |

[a] Not reported.

frames probably resulted from scale errors (imprecision in altimetry, camera tip or tilt, and refraction), which can introduce either a negative or positive bias, and the change in apparent length associated with swimming movements, which should result in a negative bias.

Finally, we compared the means of our length samples of "adult females" from the northern and central regions with comparable published data for adult females (Table 4) and found no significant differences ($t$-test; $P > 0.40$). We chose not to test for differences between our sample and published data for the neritic or southern stocks because of the small amount of data available for comparison.

*Length distribution comparisons*—Four of the five schools from the northern region were found in the shallow, nearshore habitat occupied by both the short-beaked and the larger (~28 cm for adult females; Heyning and Perrin 1991) neritic or long-beaked forms of common dolphin (Table 5). When we compared the average lengths of dolphins >150 cm and of "adult females" for the five schools from this area, it was obvious that the animals in one of the schools

*Table 5.* Depth, distance to shore, and size data for common dolphin schools photographed off of Baja California.

| School no. | Distance to shore (km) | Depth (m) | Mean length (>150 cm) | Mean length (cm) "adult females" |
|---|---|---|---|---|
| 1 | 19 | 164 | 205.6 | 206.2 |
| 2 | 27 | 182 | 180.6 | 182.3 |
| 3 | 19 | 155 | 181.3 | 179.1 |
| 4 | 16 | 150 | 177.8 | 180.3 |
| 5 | 103 | 3,300 | 168.8 | 172.8 |

*Table 6.* Summary of mean lengths and results of Tukey-Kramer pairwise tests for the northern (Nor), central (Cen) and southern (So) regions.

| | Mean length comparisons | | |
|---|---|---|---|
| Subsample criteria | Nor/Cen (cm) | Cen/So (cm) | Nor/So (cm) |
| >150 cm | 179.0/191.9** | 191.9/183.8** | 179.0/183.8* |
| >155 cm | 179.6/192.4** | 192.4/183.8** | 179.6/183.8* |
| >160 cm | 180.7/193.1** | 193.1/184.8** | 180.7/184.8* |
| >165 cm | 182.0/193.3** | 193.3/185.7** | 182.0/185.7 |
| "Adult females" | 179.2/194.8** | 194.8/184.3** | 179.2/184.3* |

* $P < 0.05$; ** $P < 0.01$.

were much larger on average (about 25 cm) than those from any of the other schools. Based on this size difference and the agreement of our data on this school with published lengths for specimens from the long-beaked form of common dolphins, we identified the animals in this school as long-beaked common dolphins and did not use these lengths in any of the regional comparisons that follow.

We conducted an ANOVA to test the hypothesis that the length samples (Fig. 4) for dolphins >150 cm from the three regions did not differ and the hypothesis was rejected ($P < 0.01$). The Tukey-Kramer *post hoc* tests found that all three regions differed significantly from one another when the minimum lengths for the samples were 150, 155, and 160 cm (Table 6). At 165 cm, the northern and southern regions no longer differed significantly, but they both differed from the central region at the $P < 0.01$ level.

When we repeated the analysis using only data for "adult females" (Fig. 5) from each region, we found significant differences ($P < 0.01$) between the central sample and the northern and southern samples. The northern and southern samples differed at the 0.05 level.

*Birth-date distributions*—Our analysis of the distribution of the back-projected birth dates revealed three distinct patterns of reproductive seasonality (Fig. 6). In the northern region most births occurred in the first six months of the year although some calving occurred throughout the year. This pattern was found to differ significantly ($P < 0.01$) when compared (modified $K$-test) with a projected uniform distribution (Fig. 7). In the central region, the back-projected birth dates were distributed throughout the year, and the modified $K$-test revealed no significant difference between the sample and a uniform pattern of births ($P > 0.10$). The sample from the southern region showed the strongest seasonality, with all calving occurring during the first six months of the year. This distribution differed significantly from the uniform ($P < 0.01$). When we repeated these analyses using birth-date distributions generated from the published average size at birth and at one year for spotted dolphins (Hohn and Hammond 1985) to determine the rate of growth, the peaks in reproduction shifted in timing but the relative patterns and test results remained the same (Fig. 8).

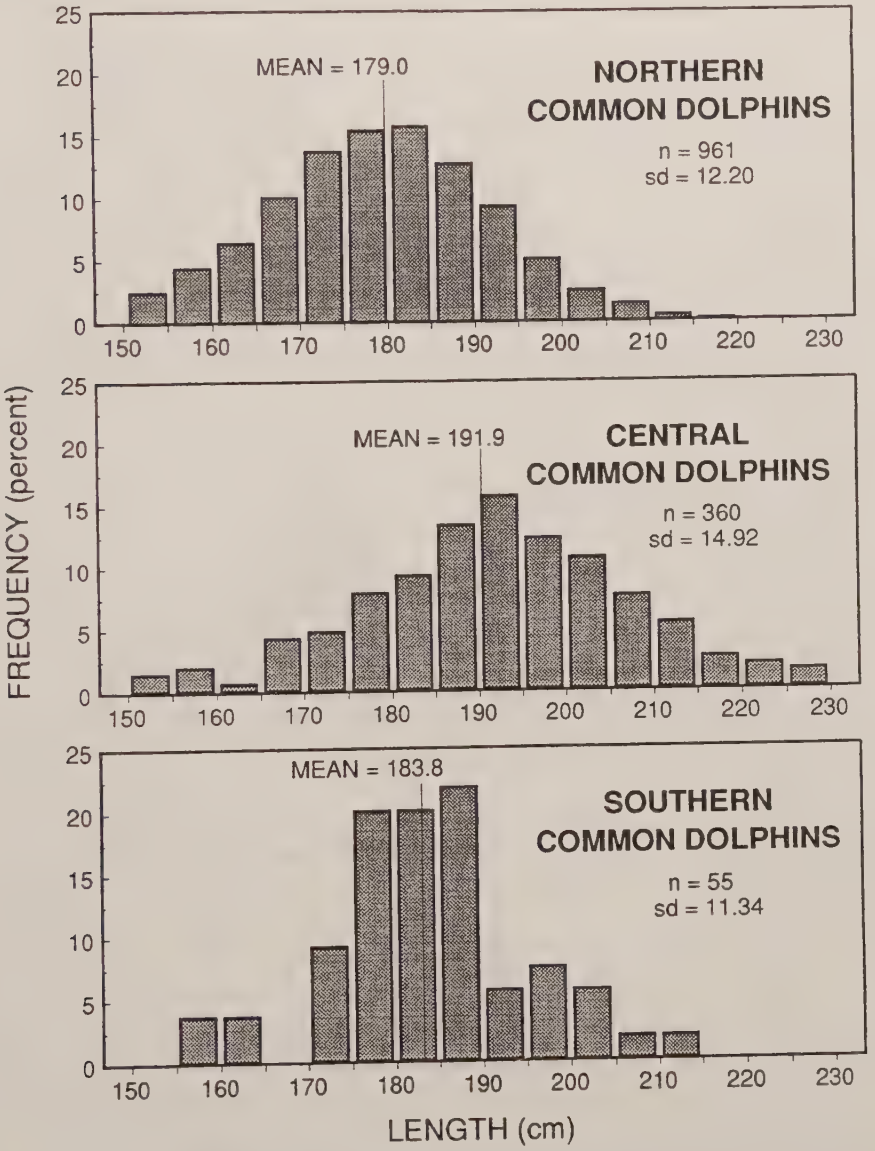

*Figure 4.* Length-frequency distributions and means for common dolphins ≥150 cm from the northern, central and southern regions. Sample size and standard deviation included for each data set.

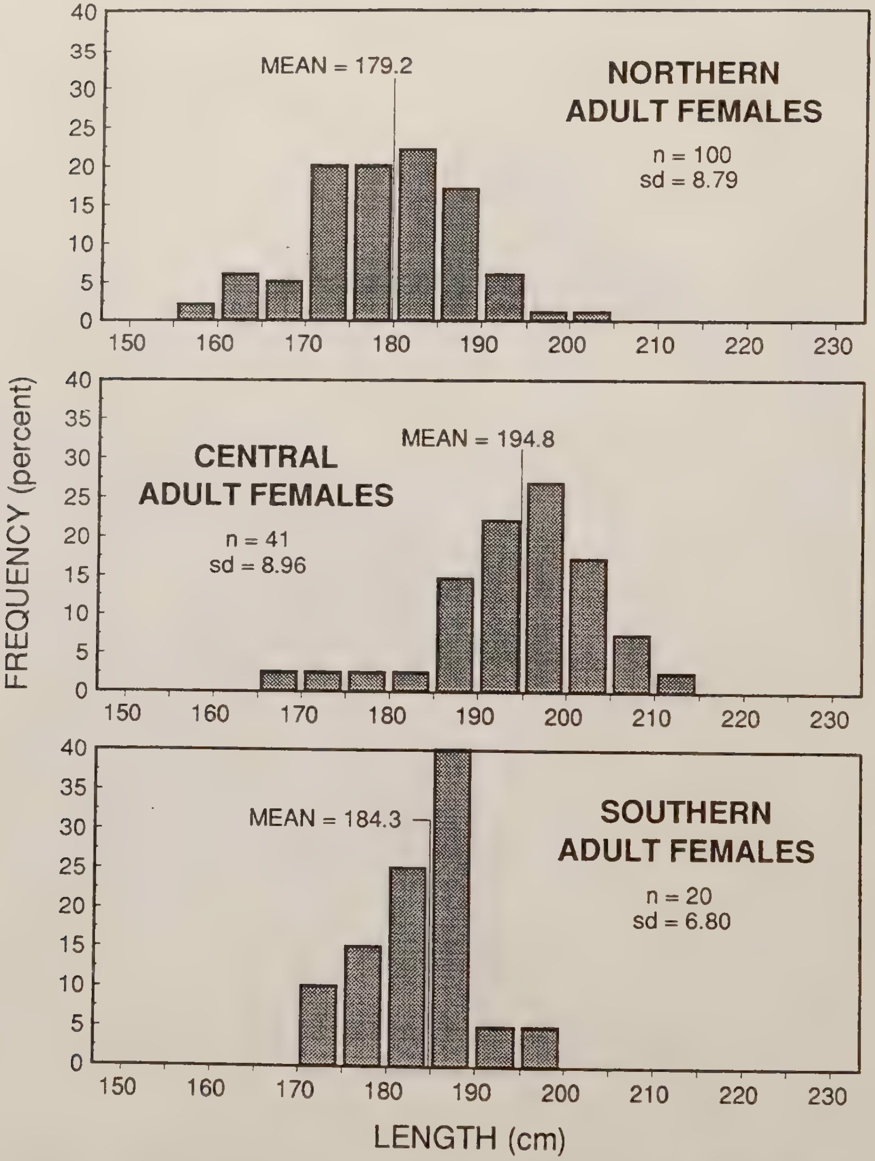

*Figure 5.* Length-frequency distributions and means for "adult females" from the northern, central, and southern regions. Sample size and standard deviation included for each data set.

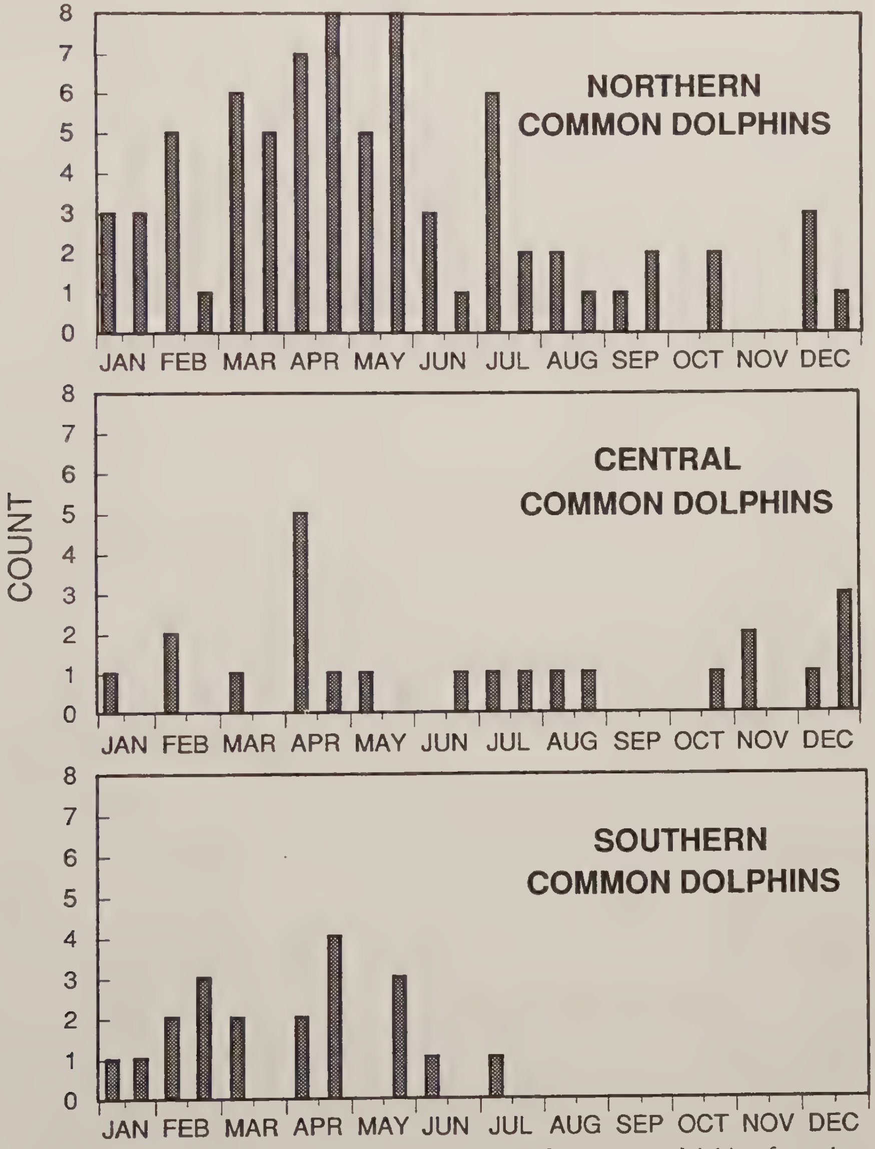

*Figure* 6. Distribution of calculated birth dates for common dolphins from three geographic areas.

## DISCUSSION

The accuracy of the target measurements (average error <1%) and the precision of repeated measures from a single image (CVs average ≈0.01) reported here are very similar to those documented in several other aerial photogrammetric

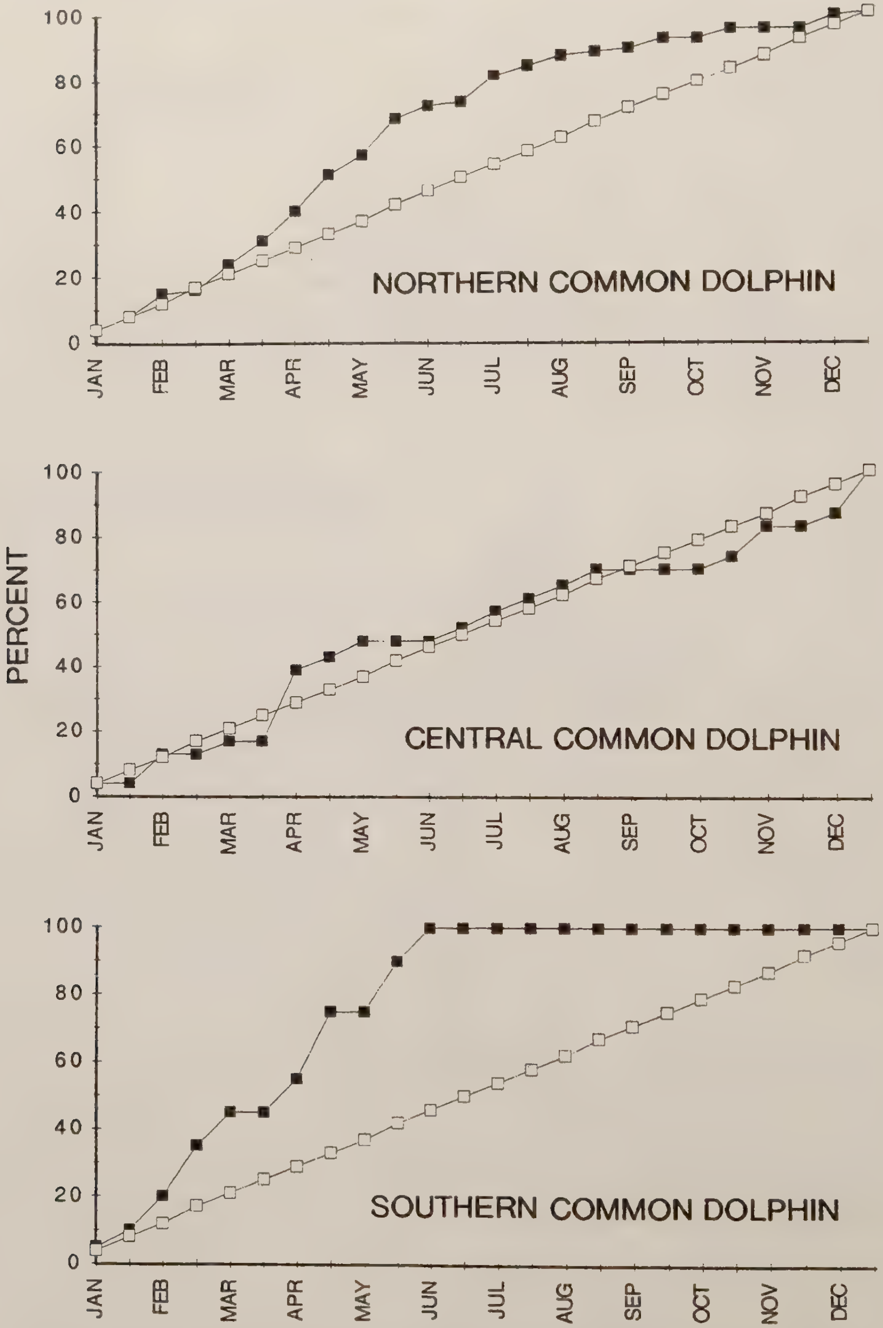

*Figure 7.* Cumulative distribution of calculated birth dates for common dolphins from the northern, central, and southern regions. Plot of open boxes represents cumulative distribution of births if births were uniform throughout the year; closed boxes represent estimated cumulative distribution of births.

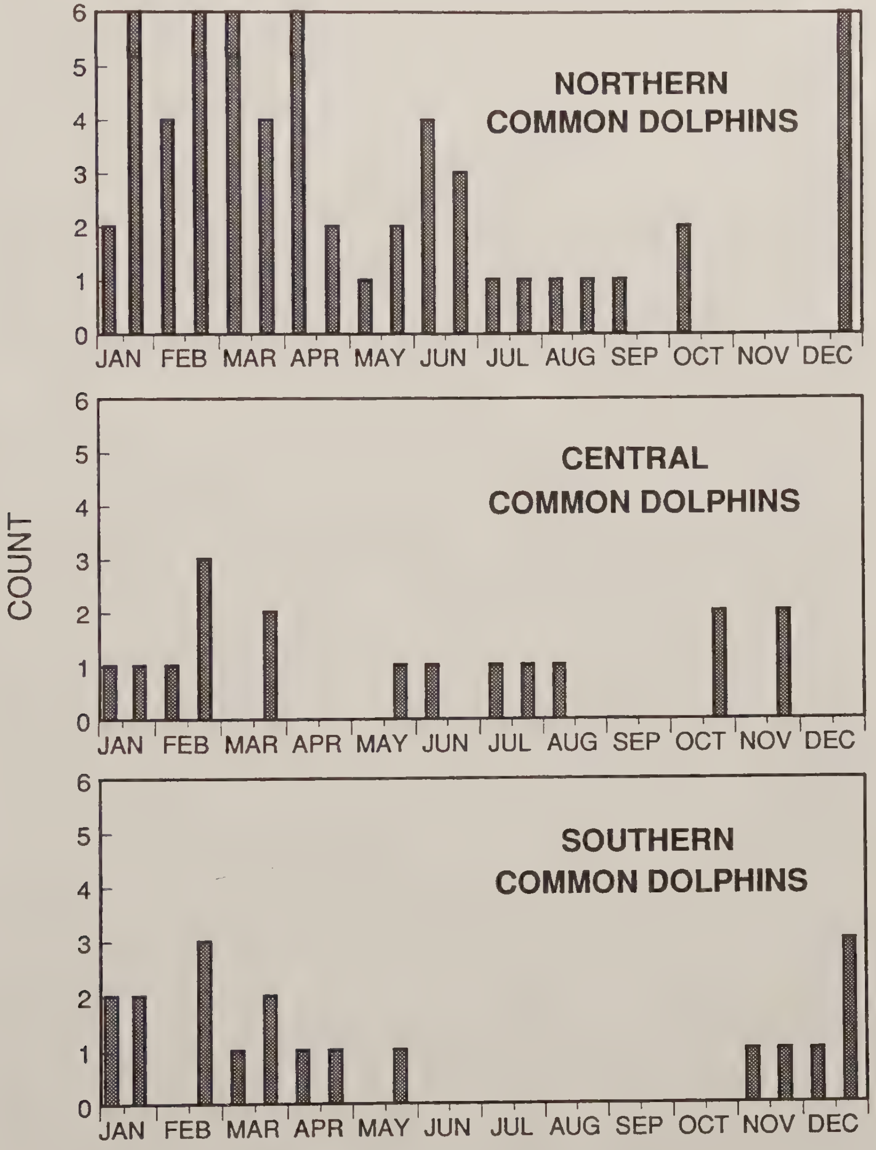

*Figure 8.* Distribution of calculated birth dates for common dolphins from three geographic areas using published data for the northern spotted dolphin to generate growth rates.

field studies (Croze 1972, Scott and Winn 1980, Cubbage and Calambokidis 1987, Koski *et al.* 1992). We also compared the lengths of dolphins measured from three or more successive frames to estimate the amount of variability in length determination resulting from errors in altitude measurement and the flex of the dolphins. As we expected, these measurements were more variable and the average of the coefficients of variation increased to 0.026. These data are comparable with average CVs of 0.014 and 0.024 for repeated photographs of gray and bowhead whales (Sumich 1984, Koski *et al.* 1992).

There are two known sources of bias in the length data that we presented in this paper. We measured to the trailing edge of the fluke rather than to the base of the fluke notch, which introduced a positive bias of about 2.5 cm for adult dolphins. Also, for an unknown proportion of the dolphins that we measured, the flex of their bodies and their orientation relative to the water's surface caused us to underestimate their length. These extremely small biases appear to have counterbalanced each other because there were no significant differences between the means of our length samples and those from previous studies that used specimens (Table 4).

We calculated the birth dates of dolphins approximately ≤1 yr old to see if there was any evidence for differences in reproductive seasonality, which could provide a barrier to gene flow between adjacent putative stocks. By this effort we are not trying to imply that we can accurately determine the age of a young dolphin from a length measurement. Rather, we think that by applying the same technique to geographically isolated groups of dolphins we can detect differences in patterns of reproduction.

In the more temperate environments to the north and south, we found a pulse in reproduction from January through July. Reproductive seasonality was strongest in the southern stock which inhabits the region that displays the widest range of oceanographic parameters of the three (Au and Perryman 1985, Fieder 1992). In the more typically tropical surface waters, which provide the habitat for the central stock, reproduction was distributed evenly throughout the year. This pattern of strong reproductive seasonality in the southern habitat in contrast to the more even distribution of births in the tropical waters to the north is similar to that demonstrated for spotted dolphins (Barlow 1984).

The data that we have reported here support the recommendations by Perrin *et al.* (1985) that common dolphins sighted within 185 km of the Pacific coast of Baja must be identified to stock based on size, beak length, and color pattern rather than by location. Based on differences in length between the northern and central putative stocks, and a hiatus in distribution between the southern and central stocks, the same authors recommended that the northern, central, and southern populations of short-beaked common dolphins should be managed as separate units. We have strengthened that argument by demonstrating differences in morphology between the southern and central regions and detecting differences in reproductive seasonality between adjacent regions. However, our data for the southern stock were drawn from only two schools that were found at the eastern edge of the distribution for this geographic form. More sampling of the southern form is needed to determine whether these data are representative of the entire southern region.

The results of the initial application of our length sampling system are very encouraging. We have developed a technique for collecting information on morphology and life history of small pelagic cetaceans that is independent of fishery-induced mortalities. This provides us with a tool for examining potential biases in our existing life history data base and the ability to sample in areas or seasons in which the fishery is not active.

## ACKNOWLEDGMENTS

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# Seabird Associations with Marine Turtles in the Eastern Pacific Ocean

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**Abstract.**—I analyzed seabird associations with marine turtles observed during 22 research vessel cruises in the eastern tropical Pacific Ocean (ETP) from 1976-1990. Of 3,032 individual turtles sighted, 176 (5.8%) were accompanied by a total of 412 birds of 13 species, with three species of boobies accounting for 63% of the associated birds. The mean number of birds per associated turtle was 2.3 (S.D. = 9.63; range 1-125); single birds occurred with 82% of the associated turtles. Seabirds utilized turtles the same way they used other floating objects on the ocean, i.e., as roosting platforms and to feed on fish that aggregated beneath them. Larger flocks (i.e., > 5 birds) occurred with turtles only when the turtles were associated with flotsam and schools of predatory fish; in each of these cases birds foraged over the fish and appeared to be only incidentally associated with turtles. The olive ridley (*Lepidochelys olivacea*) is by far the most abundant sea turtle of the five species that occur in the ETP and the only species observed with associated birds. Although millions of olive ridleys have been harvested in the ETP over the past several decades, it is still an abundant species and continues to represent a small but contributing resource for foraging seabirds, especially boobies. *Received 6 January 1991, revised 30 April 1993, accepted 16 May 1993.*

**Key Words.**— eastern Pacific, *Lepidochelys olivacea*, marine turtles, olive ridley, seabird associations.

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Seabirds are known to associate commonly with marine vertebrates, including whales, dolphins, pinnipeds and schooling fishes, in order to feed on prey made available when these animals forage near the surface (e.g., Ashmole and Ashmole 1967, Evans 1982, Burger 1988, Harrison *et al.* 1991, Pitman and Ballance 1992). Anecdotal accounts suggest that seabirds also interact with marine turtles, at least in the eastern tropical Pacific Ocean (ETP), where birds, mainly boobies, use turtles as roosting platforms at sea (Oliver 1946, Murphy 1958, Eder 1969, Marquez 1990). In other oceanic areas, references to seabirds interacting with turtles are very rare (e.g., Fritts *et al.* 1983:47-48).

Extant marine turtles comprise two families: *Cheloniidae*, with six "hard-shelled" species, and *Dermochelyidae*, the unique and monospecific leatherback. Cheloniids are cosmopolitan in tropical and warm temperate oceans, where they are largely confined to shallower continental shelf waters. The leatherback is the most pelagic sea turtle, and although it apparently prefers to forage in cool temperate waters, it nests on tropical beaches (Marquez 1990).

Five species of sea turtles occur in the ETP (Pitman 1990). The olive ridley (*Lepidochelys olivacea*) is by far the most abundant and widespread sea turtle in the warmest waters of the eastern Pacific. The loggerhead (*Caretta caretta*) replaces olive ridleys in the cooler water of the California Current off Baja California where it is locally abundant. The green turtle (*Chelonia mydas*, or sometimes referred to as *Chelonia agassizi* in the eastern Pacific) is fairly common near the continental coast or in the immediate vicinity of breeding islands (e.g., Revillagigedos, Galapagos), but very rare on the open ocean. The hawksbill (*Eretmochelys imbricata*) is easily the rarest turtle anywhere in the ETP, especially in pelagic waters. The leatherback (*Dermochelys coriacea*) is also rarely seen on the open ocean despite being readily identifiable.

Although many turtle populations in the ETP have been reduced or extirpated by human activities, some species are still common, or even abundant, in some areas of their range and thus available for interactions with seabirds. I recorded and analyzed bird associations with turtles in the ETP in order to examine the prevalence and nature of these interactions. In this paper, I describe these associations, identify the bases for their occurrence, and comment on their ecological significance.

### Study Area and Methods

The study site included an open ocean area of more than 20 million km², from California to Peru and west to approximately the longitude of Hawaii (ca. 155°W; Figure 1). Data on turtle sightings were collected opportunistically during 22 dolphin survey cruises that I participated in from 1976 to 1990. During these cruises, one or two observers searched the ocean for dolphin schools during all daylight hours, weather permitting, using mounted 20 or 25x binoculars (see Holt and Sexton 1989 for details of general survey methodology). Vessel speeds averaged 18.5 km $h^{-1}$ with cruise tracks laid out to maximize area covered within the study area. The effort in this study represents approximately 1800 days at sea.

All sightings of turtles, either by the author or reported to the author, were recorded, along with the number and identification of any associated birds. Birds were considered associated with a turtle if they were roosting on it, circling overhead, or sitting on the water within 10 m of it. The data on bird associations were biased by the fact that lone turtles were much less conspicuous than turtles with associated birds, especially if the birds were numerous or conspicuous in their activity.

Turtles were classified as either alive or dead. Floating dead turtles were difficult to distinguish from live turtles and turtles not specifically identified as dead were considered alive. Live turtles were recorded as either solitary or associated with flotsam if they occurred within 10 m of a floating object. Any predatory fish associated with turtles were identified when possible, but most of the turtles were too far from the ship to determine if fish were present or not.

At sea, the distinctive leatherback is easy to recognize, but all the remaining hardshell species of sea turtles can be difficult to identify to species under normal field conditions. Therefore, starting in 1986, as part of a project to study sea turtle distribution in the ETP, I was given the opportunity to divert the ship in order to pass close enough by individual turtles to photograph them at the surface. The photos were later examined to identify individual turtles to species. This provided me with a sample of identified individuals and eventually gave me enough experience with turtle identification to allow me to identify individuals in the field without photographing them.

The olive ridley is by far the most abundant marine turtle in the ETP as shown by nesting beach censuses (e.g., Cliffton *et al.* 1981, Cornelius 1981) and open ocean surveys (Pitman 1990, Au 1991). It was the only hardshell species I identified in the open tropical ocean, where most of my survey effort took place. Therefore, for the purposes of this study, all unidentified hardshell turtles were assumed to be that species.

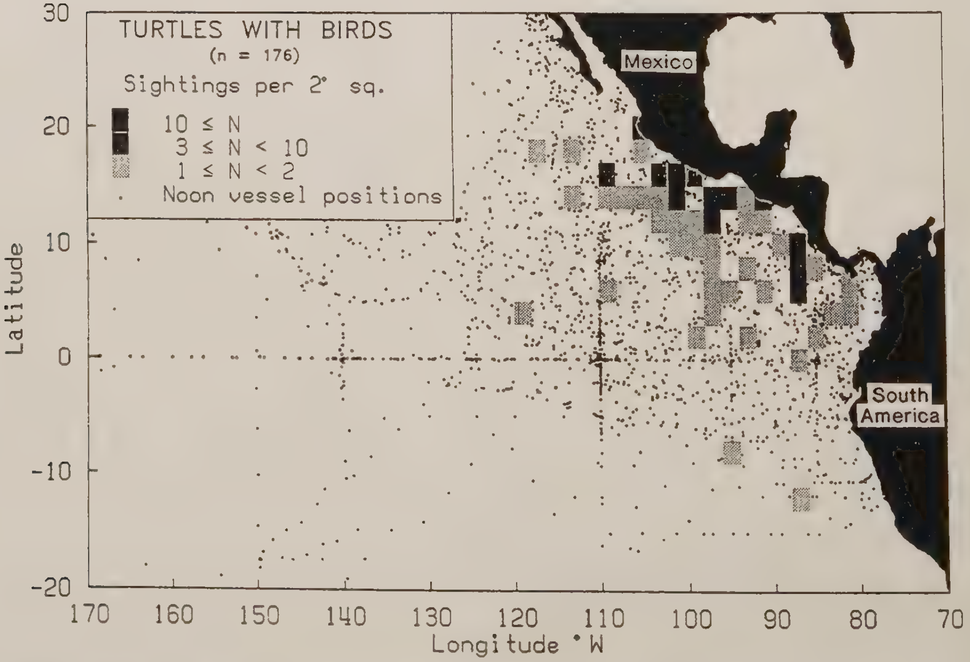

**Figure 1. Study area showing locations and numbers of turtles associated with seabirds plotted by 2° area; noon vessel positions are locations where there was survey effort but no birds were seen associated with turtles (see Pitman 1990 for additional details).**

**Table 1. Number of occurrences and mean number of birds (±SD) for seabirds occurring with different categories of sea turtles in the eastern Pacific. Bird species are arranged by functional groups (see text).**

| | Turtle Categories | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | All turtles with birds associated (N=176) | | Live turtles no flotsam (N=149) | | Dead Turtles (N=12) | | Turtles with flotsam (N=10) | | Turtles with flotsam and predatory fish (N=5) | |
| Bird species | N | mean ± SD | N | mean ± SD | N | mean ± SD | N | mean ± SD | N | mean ± SD |
| A. | | | | | | | | | | |
| Booby species<br>*Sula* spp. | 25 | 1.2 ± 0.7 | 25 | 1.2 ± 0.7 | – | – | – | – | – | – |
| Masked Booby<br>*S. dactylatra* | 79 | 1.3 ± 0.8 | 61 | 1.2 ± 0.7 | 8 | 1.0 ± 0.0 | 7 | 2.0 ± 1.1 | 3 | 1.0 ± 0.0 |
| Red-footed Booby<br>*S. sula* | 38 | 1.8 ± 2.3 | 30 | 1.2 ± 0.5 | 2 | 1.0 ± 0.0 | 4 | 2.2 ± 0.8 | 2 | 11.0 ± 1.0 |
| Brown Booby<br>*S. leucogaster* | 31 | 1.4 ± 1.6 | 24 | 1.0 ± 0.0 | 4 | 1.8 ± 1.0 | 2 | 1.5 ± 0.5 | 1 | 10.0 ± 0.0 |
| Black Tern<br>*Chlidonias niger* | 8 | 1.0 ± 0.0 | 8 | 1.0 ± 0.0 | – | – | – | – | – | – |
| B. | | | | | | | | | | |
| Wedge-tailed Shearwater<br>*Puffinus pacificus* | 3 | 29.7 ± 47.9 | 1 | 3.0 | – | – | 1 | 1.0 | 1 | 85.0 |
| Frigatebird species<br>*Fregata* spp. | 6 | 4.2 ± 3.2 | – | – | 1 | 4.0 | – | – | 5 | 4.2 ± 3.2 |
| Sooty Tern<br>*Sterna fuscata* | 3 | 10.7 ± 8.1 | – | – | – | – | – | – | 3 | 10.7 ± 6.6 |
| C. | | | | | | | | | | |
| Jaeger species<br>*Stercorarius* sp. | 1 | 1.0 | – | – | – | – | – | – | 1 | 1.0 |
| Parasitic<br>Long-tailed Jaeger<br>*S. parasiticus/longicaudus* | 1 | 1.0 | 1 | 1.0 | – | – | – | – | – | – |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Swallow-tailed Gull<br>*Creagrus furcatus* | 1 | 1.0 | – | – | – | – | – | – | 1 | 1.0 |
| Tern species<br>*Sterna* sp. | 1 | 1.0 | 1 | 1.0 | – | – | – | – | – | – |
| Artic Tern<br>*S. paradisaea* | 1 | 1.0 | 1 | 1.0 | – | – | – | – | – | – |
| Bridled Tern<br>*S. anaethetus* | 1 | 1.0 | 1 | 1.0 | – | – | – | – | – | – |
| White Tern<br>*Gygis alba* | 1 | 1.0 | – | – | – | – | – | – | 1 | 1.0 |
| Noddy species<br>*Anous* sp. | 1 | 7.0 | – | – | – | – | – | – | 1 | 7.0 |
| Black Noddy<br>*A. tenuirostris* | 1 | 1.0 | 1 | 1.0 | – | – | – | – | – | – |
| D. | | | | | | | | | | |
| All birds | 176 | 2.3 ± 9.6 | 149 | 1.2 ± 0.7 | 12 | 1.7 ± 1.4 | 10 | 2.7 ± 1.4 | 5 | 36.6 ± 44.8 |
| Number of bird species | 176 | 1.1 ± 0.6 | 149 | 1.0 ± 0.2 | 12 | 1.2 ± 0.4 | 10 | 1.4 ± 0.5 | 5 | 3.8 ± 1.6 |

## RESULTS

A total of 3,032 individual turtles were sighted, including 277 (9.1%) olive ridleys, 42 (1.4%) loggerheads, 31 (1.0%) leatherbacks, 22 (0.7%) greens, 1 hawksbill, and 2,659 (87.7%) unidentified hardshell turtles. Of these, 176 individual turtles (5.8%) had associated birds (Table 1). Birds were associated with 37 olive ridleys and 139 unidentified hardshell turtles; no other turtle species was observed with birds. There was an overall mean of 2.3 birds/associated-turtle (SD = 9.6), ranging from 1 to 125, with a mode of 1. The mean number of bird species associated with individual turtles was 1.1 (SD = 0.6), with a range of 1-6. Although seabirds associated with marine turtles throughout much of the ETP (Fig. 1), associations were more common closer to the coast of the Americas, where turtles were more abundant (Pitman 1990).

A total of 412 individual birds of 13 species were associated with turtles (Table 1). Boobies, induding Brown (*Sula leucogaster*), Red-footed (*S. sula*) and Masked (*S. dactylatra*), were by far the most commonly associated species: they accounted for 63% of the individual birds that occurred with turtles and they were present with 91% of the turtles that had associated birds.

Bird species associated with turtles comprised three general categories. The first included the species which were associated with turtles most often, but typically in small numbers (mean < 2 birds/associated-turtle) (Table 1a). These included all three booby species and the Black Tern (*Chlidonias niger*). Olive ridleys often basked at the surface and these birds were most often seen perching on their exposed carapaces. There was room for only one bird at a time to stand on top of the small, rounded portion of a turtle's exposed carapace, and single birds were present in 82% of the cases.

The second group of turtle-associated birds was comprised of species that occurred less frequently with turtles, but in larger numbers per turtle when they did. These species were Wedge-tailed Shearwaters (*Puffinus pacificus*), frigatebirds (*Fregata* spp.) and Sooty Terns (*Sterna fuscata*) (Table 1b). This group was further distinguished by the fact that none of these birds were ever seen roosting on turtles, and 94% of all the individuals of these species that occurred with turtles did so when both flotsam and schools of predatory fish were also present. The third category was comprised of species that were recorded only once with turtles, and usually with only one bird present (Table 1c).

Although not statistically significant, there was a trend of increasing number of associated birds and number of bird species from solitary turtles, to dead turtles, to turtles associated with flotsam (Table 1d). Every bird species recorded with turtles more than once, except Black Tern, was more numerous when turtles were associated with flotsam (Table 1a,b,c). Compared with other turtle categories, turtles associated with flotsam and tunas had the largest and most diverse bird flocks with significantly more individual birds (Single Factor ANOVA, F = 34.2, $P < 0.001$) and species of birds (Single Factor ANOVA, F = 101.7, $P < 0.001$). The five largest flocks associated with turtles, including all flocks of over five birds, were associated with flotsam that had predatory fish schools underneath.

Two general categories of schooling fishes associated with turtles, which provided different foraging opportunities for birds: small baitfish and larger schooling predators. Schools of small baitfish were often seen swimming near turtles that the ship passed close by. The species identified included flotsam fish (*Psenes cyanophrys*), pilotfish (*Naucrates ductor*), pelagic triggerfish (*Canthidermis maculatus*), tripletail (*Lobotes surinamensis*), and numerous others. These fishes seemed to be seeking protection because they often responded to the vessel, and predatory fish, by forming tight schools directly underneath the turtle. The same behavior was observed when the ship passed by flotsam with baitfish associated.

Birds, especially boobies, were observed preying upon these fish. On calm days when turtles were present, it was fairly common to see a flying booby change course to approach a turtle at the surface. The booby would either land on the turtle or on the water close by, plunge into the water next to it, or circle overhead once or twice and continue on its way. Boobies fed most often around turtles by plunge-diving within 2 m of them; on several occasions I saw boobies catch fish this way. Although plunge-diving was the most common foraging behavior, birds were also able to use other foraging methods to catch fish associated with turtles. For example, on two separate occasions I saw a single booby land next to a turtle, stick its head in the water, under the turtle, and pull out a fish which it swallowed. Another time I saw three Wedge-tailed Shearwaters making shallow dives directly undeneath a turtle, but it was impossible to tell if they were successful in catching fish.

The second category of fish that associated with turtles usually occurred when turtles were associated with flotsam and was comprised of larger schooling predators that included mainly tunas. (At these sites, we caught yellowfin tuna [*Thunnus albacares*], skipjack [*Katsuwonus pelamis*], black skipjack [*Euthynnus lineatus*], mahi mahi [*Coryphaena hippurus*] and wahoo [*Acanthocybium solandri*]). The birds in these flocks (mainly shearwaters, terns, frigatebirds, and also boobies) focused on the feeding activity of the foraging fish and fed on prey scattered by them.

The only other kind of foraging interaction I observed between birds and turtles at sea involved a single Parasitic or Long-tailed Jaeger (*Stercorarius parasiticus* or *S. longicaudus*) sitting on the water next to an olive ridley and picking at epibionts along the edge of the carapace (probably taking either commensal crabs or soft barnacles). This behavior was observed only once.

## DISCUSSION

The only species of sea turtle that seabirds were seen associated with in the eastern Pacific was the olive ridley. This was probably because it was by far the most abundant species in the study area (Pitman 1990), and also because of its habit, possibly unique among sea turtles, of regularly basking at the surface (Marquez 1990; pers. obs.).

ETP seabirds used sea turtles the same way they used other floating objects and the same way Atlantic seabirds use patches of *Sargassum* i.e., as roosts and to feed on fish that aggregate underneath them (Haney 1986).

### Roosting

Most bird-associated turtles were accompanied by single birds, nearly all of which were roosting on turtles floating at the surface. One reason for this roosting behavior may be that seabirds sitting on the water, especially in the tropics, are vulnerable to attacks from sharks (e.g., Nelson 1978:921, Schreiber and Chovan 1986). Roosting on floating objects reduces this threat, and many seabirds in the ETP, especially boobies, will roost on any floating object large enough to support them (pers. obs.), including sea turtles. Haney (1986) also suggested that birds such as the Black Tern may seek out dry roosts for resting and preening because their plumages are less water-resistant.

### Feeding

Unlike large schooling fish and mammals that drive prey to the surface making it available to birds (e.g., Au and Pitman 1986), turtles provided feeding opportunities for birds mainly by acting as passive fish aggregators, or FADs (Fish Aggregation Devices; see, for example, Rountree 1989). On the open ocean, small fishes are often attracted to floating objects (Hunter and Mitchell 1966, Gooding and Magnuson 1967), including turtles (Gooding and Magnuson 1967, Balazs 1981, this study). These fish seek out floating objects and form resident schools, presumably for protection and feeding. Many tropical seabirds, especially boobies, are attracted to floating objects on the open ocean where they prey upon these associated fishes (Haney 1986; pers. obs.).

Floating objects often attracted a second fish assemblage composed of larger, schooling, predatory fishes, which were observed with turtles only when the turtles associated with flotsam. Associations between birds and turtles in these cases were probably largely coincidental, because both turtles and predatory fish such as tuna are independently attracted to flotsam (Greenblatt 1978, Pitman 1990), and birds appeared to be mainly attracted to the feeding activities of the tuna.

The ability of floating FADs (including turtles) to attract fish (and therefore birds) is related to characteristics of the object, with larger, more stationary objects being more attractive (Tsukagoe 1981, Rountree 1989). This may explain the trend of increasing bird numbers and species associated with live turtles, dead turtles and turtles associated with flotsam, respectively.

Although the percentage of turtles with associated birds and the number of birds per associated turtle were both quite small, by dint of sheer numbers alone the olive ridley probably represents a more important resource for ETP seabirds than my small sample (3000) of turtle sightings suggests. For example, Richard and Hughes (1972) reported that two separate nesting beaches in Costa Rica each had over 100,000 olive ridleys aggregated offshore during peak nesting periods. And Cliffton *et al.* (1981) estimated that there was a minimum of 10,000,000 olive ridleys in Mexican waters prior to 1950, when commercial exploitation began. Populations of these magnitudes suggest a resource that is, or possibly was, of more than passing importance for ETP seabirds.

Several of the largest olive ridley rookeries in the eastern Pacific have been decimated by commercial harvests that, until recently, annually took hundreds of thousands of adult turtles and millions of eggs (Cliffton *et al.* 1981, Green and Ortiz-Crespo 1981). Carr (1972) estimated that more than one million olive ridleys were landed in Mexico in 1968 alone. Loss of marine turtles on this scale, regrettable in its own right, has undoubtedly reduced some of the options for foraging seabirds in the ETP. Recent bans on commercial sea turtle harvesting in the ETP by the two main countries involved, Mexico and Ecuador (Aridjis 1990, Frazier and Salas 1982 ), should benefit both marine birds and turtles.

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# The Lobster and Shrimp Fisheries in Hawaii

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*ABSTRACT — A description of the lobster and deepwater shrimp fisheries in Hawaii, addressing harvest levels, biology, and research, is presented. Both fisheries are trap fisheries. The lobster fishery is a limited entry fishery with 1991 landings of 200 metric tons. The shrimp fishery is unregulated, with very sporadic effort, and annual landings below 200 metric tons.*

## The Lobster Fishery

### Introduction

The commercial lobster fishery in Hawaii is a trap fishery which harvests several lobster species in the Northwestern Hawaiian Islands (NWHI)—an isolated range of islands, islets, banks, and reefs extending 1,500 n.mi. northwest, from Nihoa Island to Kure Atoll (Fig. 1). The fishery targets two species: the endemic spiny lobster *Panulirus marginatus* (Quoy and Gaimard, 1825) and the common slipper lobster *Scyllarides squammosus* (Milne-Edwards, 1837) (Fig. 2,3). Two other species—the ridgeback slipper lobster *S. haanii* (de Haan, 1841) (Morin and MacDonald, 1984) and the Chinese slipper lobster *Parribacus antarcticus* (Lund, 1793)—are caught incidentally in low abundance.

Lobster concentrations in the NWHI were documented by research cruises in 1976, and commercial trapping began in 1977 (Uchida and Tagami, 1984). Since 1983, the lobster fleet has ranged from 9 to 16 vessels (15 to 35 m long), each averaging 3 trips per year. A typical vessels sets about 800 traps per day and remains at sea almost 2 months per trip. The NWHI lobster fishery is Hawaii's most valuable demersal fishery; in recent years, annual landings have averaged about 600 metric tons (t) (1 million lobsters), valued at about $6 million U.S. ex-vessel (Fig. 4). Since 1988, about 80% of the landings have been spiny lobster (Polovina[1]).

A commercial shellfish trap made by Fathoms Plus[2] is used by all the fishermen. This is a dome-shaped, single-chambered trap made of molded black polyethylene which measures 980 × 770 × 295 mm, with a mesh size of 45 × 45 mm (inside dimensions). Each trap has two entrance cones located on opposite sides. Each trap also has two escape vent panels each consisting of four 67 mm diameter circular vents located on opposite sides to facilitate the escapement of sublegal lobsters (lobsters under minimum legal harvest size). The traps are typically baited with chopped mackerel (*Scomber* sp.) and fished in strings of several hundred traps per string most frequently set in depths from 20 to 70 m.

### Synopsis of the Fishery

The historical landings from the lobster fishery exhibit a classical trend of a developing fishery with a period of low catches at the beginning of the fishery (1977–83) followed by a rapid increase in landings as more vessels entered the fishery and markets were developed (1984–86) and most recently a decline in landings as the population is reduced by overfishing (1987–91) (Fig. 4). In the early years of the fishery (1977–84) and since 1988, landings have been about 80% spiny and 20% slipper lobsters. However, for a three-year period from 1985 to 1987 the fishery targeted and largely depleted a previously lightly exploited population of slipper lobsters.

Stock assessment has used the annual catch of spiny and slipper lobsters and trapping effort data from the commercial logbooks since 1983 (Table 1).

**Table 1.—Annual landings of spiny and slipper lobsters (in 1,000's), trapping effort (in 1,000's trap-hauls), and the percentage of spiny lobster in the landings, 1983–90.[1]**

| Year | Spiny lobster | Slipper lobster | Total lobsters | Trapping effort | CPUE | Spiny lobster % |
|---|---|---|---|---|---|---|
| 1983[2] | 158 | 18 | 176 | 64 | 2.75 | 90 |
| 1984 | 677 | 207 | 884 | 371 | 2.38 | 78 |
| 1985 | 1022 | 900 | 1922 | 1041 | 1.83 | 53 |
| 1986 | 843 | 851 | 1694 | 1293 | 1.31 | 50 |
| 1987 | 393 | 352 | 745 | 806 | 0.92 | 53 |
| 1988 | 888 | 174 | 1062 | 840 | 1.26 | 84 |
| 1989 | 944 | 222 | 1166 | 1069 | 1.09 | 81 |
| 1990 | 591 | 187 | 778 | 1182 | 0.66 | 76 |
| 1991[3] | 131 | 35 | 166 | 292 | 0.56 | 79 |

[1] Data were provided to the Honolulu Laboratory, National Marine Fisheries Service, as required by the Crustacean Fishery Management Plan of the Western Pacific Regional Fishery Management Council.

[2] April-December 1983.

[3] January-May, November-December 1991.

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[1] J. J. Polvina. 1991. Status of lobster stocks in the Northwestern Hawaiian Islands, 1990. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent. Admin. Rep. H-91-04, 16 p.

[2] Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

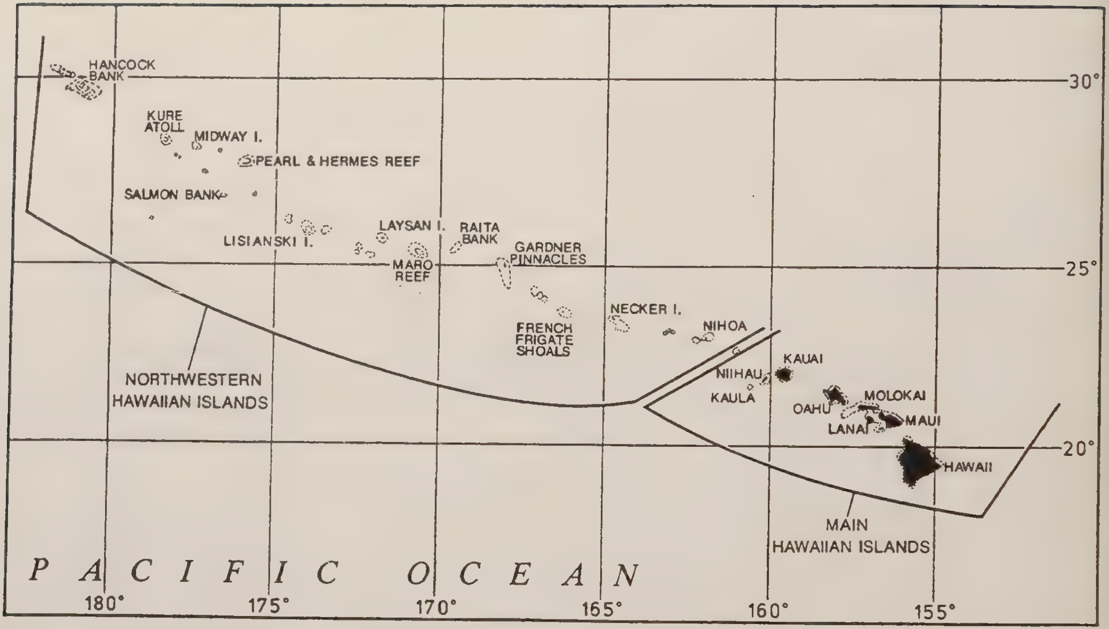

Figure 1.—The Hawaiian Archipelago, including the Northwestern Hawaiian Islands.

Both spiny and slipper lobsters may be caught in the same trap but fishermen can alter the proportion of each species by selecting the trapping area and depth. Logbooks record only the number of traps hauled and do not specify when effort targets spiny or slipper lobster. Since 1983 when logbook reporting was in effect, the combined catch per unit effort (CPUE) for legal slipper and spiny lobsters has declined from 2.75 to 0.56 lobster per trap-haul (Fig. 4).

Stock assessment of the lobster resource is hindered by the relatively short catch and effort time series and our inability to age lobsters. A dynamic production model, fit to the combined spiny and slipper lobster catch and effort data for the entire NWHI, estimates an equilibrium production curve with a maximum sustainable yield of 900,000 lobsters/year from a fishing effort of 740,000 trap-hauls, resulting in a CPUE of 1.22 lobsters/trap-haul (Polovina[1]). A CPUE time-series model estimates the annual instantaneous natural mortality ($M$) at 0.7/year and catchability ($q$) at $1.0 \times 10^{-6}$ (Polovina[1]). Thus the 1990 fishing effort of 1.2 million trap-hauls corresponds to a fishing mortality ($F$) of 1.2/year or 1.7 times $M$. Based on the minimum harvest sizes and this level of fishing mortality, the spawning stock biomass per recruit is estimated at 40% of the level in the absence of fishing.

Both the level of fishing mortality relative to natural mortality and the relative spawning biomass suggest that fishing effort alone was not sufficient to cause the decline in CPUE observed in 1990 and 1991. Current research suggests this decline is the result of poor recruitment (due to oceanographic conditions) at some banks which resulted in a concentration of fishing effort at the remaining banks where recruitment was strong.

## Research

After the initial research cruises documented lobster concentrations in the NWHI in 1976, research focused on the biology of the spiny lobster *Panulirus marginatus*. Tagging studies at Kure Atoll and French Frigate Shoals estimated a von Bertalanffy growth curve for growth (in carapace length) to have a parameter $K$ of 0.31/year with an asymptotic carapace length of 13.2 cm, a mean natural mortality estimate of 0.37/year, and estimates for the ages at the onset of sexual maturity of 2.7 and 1.7 years for males and females, respectively (MacDonald, 1984). Trapping surveys mapped the spatial distribution of *P. marginatus* in the NWHI and indicated that the highest catch rates ranged from depths of 55–73 m in the southeastern portion of the NWHI to 19–54 m in the northwestern portion of the Hawaiian Archipelago (Uchida and Tagami, 1984). The settlement of post-larval lobster, puerulus, were monitored at Kure Atoll, French Frigate Shoals, and Oahu with surface collectors (MacDonald, 1984). Puerulus settlement appeared seasonal at the ends of the Hawaiian Archipelago; the greatest settlement occurred in the summer at Kure Atoll and in the winter at Oahu while at French Frigate Shoals, more centrally located, settlement appeared more uniformly throughout the year (MacDonald, 1986).

Research conducted during 1984–87 developed escape vents to reduce the catch and hence mortality of sub-

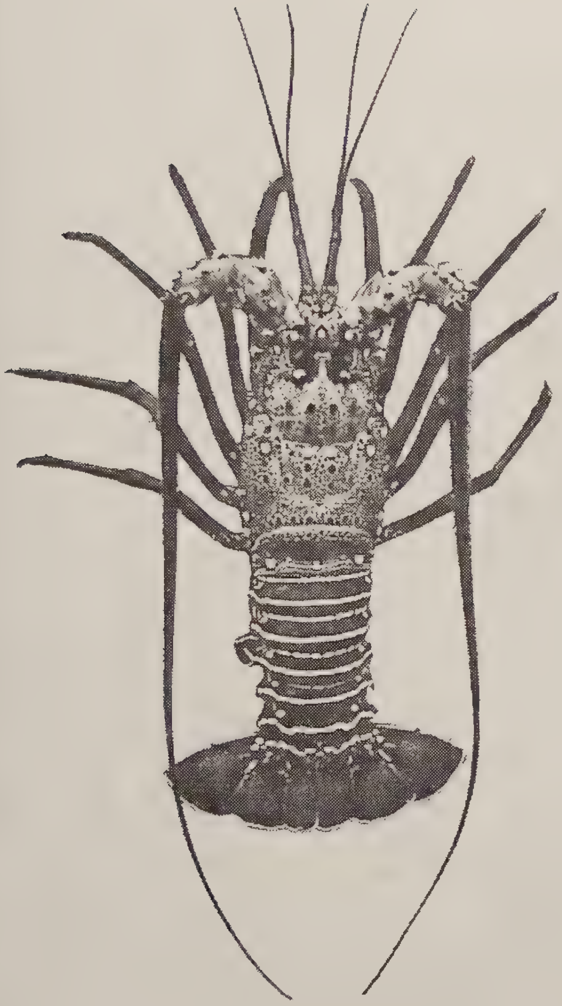

Figure 2.—The spiny lobster, *Panulirus marginatus*.

legal spiny lobster (<50 mm tail width) and sublegal slipper lobster (<56 mm tail width) without reducing legal catches. A circular vent design takes advantage of the different morphology of the spiny and slipper lobsters to allow escapement at different tail sizes for each species. Specifically, research found that traps equipped with two vent panels consisting of four 67 mm diameter circles placed at the bottom of the trap caught 83% and 93% fewer sublegal spiny and slipper lobsters than did nonvented control traps, without significantly reducing legal catches of either species (Everson et al., In press).

An estimated 2,000 plastic traps are lost annually in the NWHI. Concern has been raised that lobsters entering those lost traps may be unable to exit and therefore die. Recent field and tank studies have investigated whether lobsters can escape unbaited lobster traps. The results indicate that lobsters using the traps for shelter are able to exit, and no mortality due to the retention of slipper or spiny lobster in traps was observed (Parrish and Kazama, 1992).

Ongoing research is directed toward understanding the factors responsible for observed spatial and temporal variation in adult lobster abundance within the Hawaiian Archipelago. Results from larval tows and studies on local oceanography suggest that long-term differences in lobster densities between banks in the NWHI are not due to local larval densities but to differences in the amount of relief provided by the benthic habitat on the banks.

Temporal variation in spiny lobster stocks at the two most productive banks in the fishery, Maro Reef and Necker Island, has been studied with both commercial and research data. Research and commercial trapping data both show a wide variation in recruitment to the fishery for spiny lobster at Maro Reef relative to Necker Island, 360 n.mi. to the southeast. A high correlation is observed between recruitment to the fishery at Maro Reef and the relative sea level between French Frigate Shoals and Midway Island four years earlier. Geosat altimeter data indicate that the variation in relative sea level between French Frigate Shoals and Midway is linked to the El Niño Southern Oscillation (ENSO). The mechanisms responsible for the apparent link between sea level and lobster recruitment are not known and are the subject of current research. However, the sea level index may prove to be a useful forecast of recruitment to the fishery at Maro Reef four years later (Polovina and Mitchum, 1992).

One economic study (Clarke and Pooley, 1988) has examined the return on investment as a function of vessel size. The most profitable vessels in the fleet are the midsize vessels. These vessels are 20–30 m long, have 5–9 crew members, and are able to set 600–820 traps per day. Larger vessels face cost constraints while smaller vessels face operational problems.

## Management

The fishery has been managed under Federal jurisdiction with a fishery

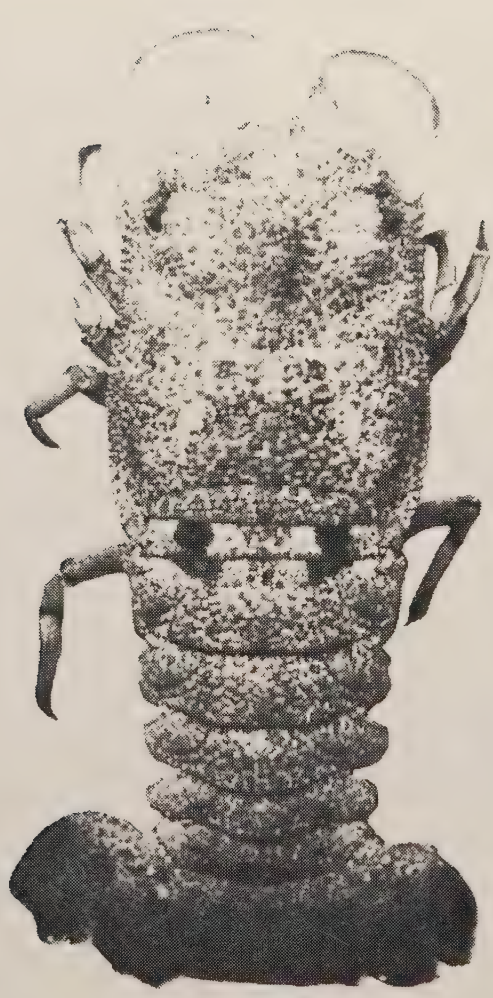

Figure 3.—The slipper lobster, *Scyllarides squammosus*.

management plan (FMP) administered by the Western Pacific Regional Fishery Management Council (WPRFMC) since 1983. Currently the plan prohibits the harvest of slipper lobster (*S. squammosus*) with a tail width of <56 mm and spiny lobster (*P. marginatus*) with a tail width of <50 mm, prohibits the retention of egg-bearing females, requires that all traps have escape vents to reduce handling and release-induced mortality on sublegal lobsters, and mandates that vessels submit logbooks recording daily catch and trapping effort. A decline in CPUE from 1.25 lobster per trap-haul in 1988 to 0.6 in 1990 as well as concerns that vessels from other fisheries in worse condition were considering entering the lobster fishery, motivated the fishermen to work with the WPRFMC to develop a limited entry and harvest quota plan. Further, to protect the spawning biomass of the stock while the plan was being developed the WPRFMC passed emergency regulations to close the fishery for 6 months (May through October, 1991). In March 1992, the lobster FMP was amended to include provisions for a limited entry system for a maximum of 15 vessels, an annual fleet harvest quota, and a closed season from January through June to protect the spawning biomass before the summer spawning. The quota is set to achieve an average CPUE over the fishing season of 1.0 lobster per trap-haul. A preseason quota is set using an estimate of the population size at the end of the previous fishing season and estimates of natural mortality and recruitment. A final quota is set after the first month of fishing based on the CPUE during that month. Information from research surveys can also be used in the quota calculations. Currently, fishermen and managers are considering whether an individual quota would be an improvement over the current fleet quota.

The lobster fishery has sufficient management regulations, which if applied correctly, should make the fishery sustainable and economically profitable. However, environmental factors may result in both considerable annual as well as decadal-scale variation in the exploitable lobster population and hence landings.

## The Shrimp Fishery

Deepwater pandalid shrimp are found in some abundance throughout the tropical and subtropical Pacific (King, 1984; Moffitt and Polovina, 1987). In Hawaii, research trapping showed that *Heterocarpus laevigatus* (Fig. 5) and the smaller and more shallow dwelling species, *H. ensifer*, could be readily caught in the depth range 350–825 m in baited traps (Struhsaker and Aasted, 1974). During the past decade there have been two periods when the resource, particularly the more valuable species *H. laevigatus*, has been the target of fishing. In the early 1980's a small trap fishery was initiated around the main Hawaiian Islands. The vessels typically used large, pyramid-shaped traps with a volume of almost 2 m$^3$, and a large vessel might set up to 50 traps a day (Tagami and Barrows,

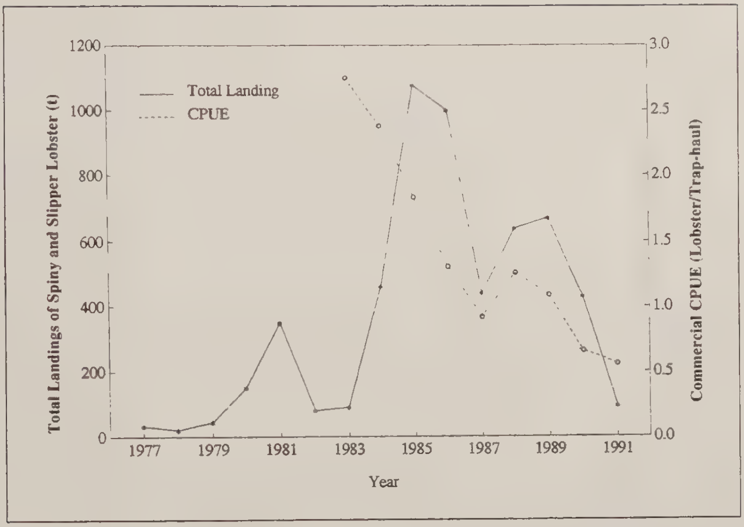

Figure 4.—Total lobster landings and commercial catch per unit effort (CPUE) from the lobster fishery in the Northwestern Hawaiian Islands. Data since 1983 are based on vessel logbooks required under the fishery management plan.

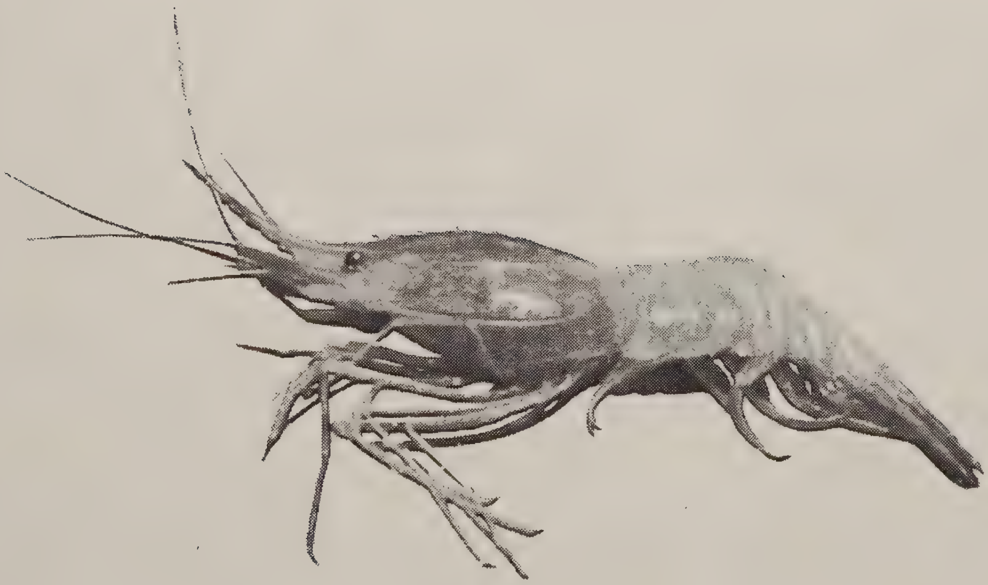

Figure 5.—The deepwater shrimp, *Heterocarpus laevigatus*.

1988). Landings from this fishery peaked in 1984 at over 190 metric tons of *H. laevigatus* with an ex-vessel value of $1.5 million ($7.85/kg) from 7 vessels, 23–40 m in length (Ralston and Tagami, 1992). However by the late 1980's most of the vessels had left the fishery as declining catch rates and the high cost of the deep trapping made the fishery unprofitable. There was a resurgence in the fishery in 1990, when landings of over 100 t were reported, primarily the result of intensive fishing by a single vessel but this level of production was not sustainable at a profitable CPUE[3]. Currently there are no management regulations for this resource.

Recent research has conducted submersible surveys of shrimp densities on different habitats and estimated shrimp biomass from an intensive trapping depletion study (Moffitt and Parrish, 1992; Ralston and Tagami, 1992). The submersible surveys observed that *H. ensifer* tended to group around large anemones and other benthic relief over an otherwise flat, sandy bottom and were very active in the presence of a baited trap (Gooding et. al., 1988; Moffitt and Parrish, 1992). However, *H. laevigatus* were solitary and showed little activity around baited traps. Greater densities of *H. laevigatus* were observed on volcanic than on coralline substrata (Moffitt and Parrish, 1992). The depletion study based on intensive trapping estimated a catchability coefficient which when applied to trapping data around the main Hawaiian Islands estimated an exploitable biomass of *H. laevigatus* of 271 t (Ralston and Tagami, 1992).

While the deepwater shrimp resource may support a very limited local fishery or perhaps periodic heavy pulse fishing, it is unlikely to be the object of heavy sustained exploitation. Initial high catch rates appear to drop rapidly, gear loss is appreciable and costly due to the trapping depths, and markets are not well established.

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# Economics and Hawaii's Marine Fisheries

SAMUEL G. POOLEY

*ABSTRACT—This paper reviews economic research conducted on Hawaii's marine fisheries over the past ten years. The fisheries development and fisheries management context for this research is also considered. The paper finds that new approaches are required for marine fisheries research in Hawaii: A wider scope to include other marine resource and coastal zone issues, and increased and closer collaboration between researchers and the fishing community.*

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## Introduction

Fishing and seafood consumption permeate society in Hawaii, although neither the total volume of seafood harvesting nor the market value of seafood is a particularly large share of the state's economic activity.[1] Seafood consumption is an integral aspect of Hawaii's culture, from traditional Polynesian uses of nearshore and reef species to the importance of seafood in Asian cultures. As a result of cultural adaptation by the rest of the population and energetic promotion of local seafood in restaurants oriented toward tourism, per capita seafood consumption in Hawaii is high, and a very large percentage is fresh fish (Higuchi and Pooley[2]; East-West Research Inst.[3]).

Fishing and seafood marketing also have been important bridges into commercial society for several immigrant groups, from the Japanese, Chinese, and Portuguese who came to Hawaii as plantation workers at the turn of the century to Koreans and North Americans who came for more varied reasons over the past 20 years. Fishing has also been important in tourism, particularly for Kailua-Kona on Hawaii (the Big Island), through the promotion of deep-sea fishing and sport fishing tournaments.

Hawaii is not the "paradise" promoted by the tourism industry, although probably for most people living here it is the only place to live. Hawaii is a densely populated state,[4] with an economy dominated by tourism (as much as 50% of the gross state product) and with a natural resource policy dominated by land use and coastal zone development issues. Nonetheless, subsistence fishing in rural areas and recreational fishing for city residents are important releases from urban culture, as well as sources of food and income.

With this in mind, the following sections attempt to delineate important components of the economics of Hawaii's fisheries. However, there has been no comprehensive survey of recreational and subsistence fishing activity in Hawaii, and economic surveys have been episodic. Thus the information with which to estimate the economic value of the Hawaii fishery is limited.

## Economic Values

Determining the economic value of Hawaii's marine fisheries is not simply a process of adding up commercial values, nor the straightforward valuation of subsistence and recreational resources and cultural practices, nor even a recitation of the kind of economic processes which affect the use, development, and management of these resources. The common yardstick for determining the economic value of commercial fisheries is ex-vessel revenue from the sale of harvested fish (and shellfish). In Hawaii, where there is essentially no processing industry, this is a good start. Ex-vessel revenue from Hawaii's commercial fisheries has been estimated at $50 million in 1990 (Pooley, unpubl. data).[5] This revenue was generated from 21 million pounds (9,500 t) of marine fish landed in Hawaii by Hawaii-based fishing vessels. The composition of ex-vessel revenue by the major fleet components is shown in Figure 1.

However, there are three additional direct components to the economic value of Hawaii's marine fisheries: recreational fishing values, subsistence fishing values, and charter fishing values.[6] First, it is important to realize that the distinction between "commercial" and "recreational and subsistence" fishing in Hawaii is a weak distinc-

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[1] The ex-vessel value of Hawaii's commercial fishery is less than 2/10% of gross state product, while the wholesale value of the seafood market (including imports) is less than 5/10%. (General statistics for Hawaii are taken from the State of Hawaii Data Book. 1990. Dep. Planning and Econ. Development. Honolulu, Hawaii.)

[2] W. K. Higuchi and S. G. Pooley. 1985. Hawaii's retail seafood volume. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-85-06, 16 p.

[3] East-West Research Inst. 1989. Hawaii seafood consumption: a survey of seafood consumption in Hawaii. Contract Rep., State of Hawaii, Dep. Business and Economic Development, Honolulu, Hawaii.

[4] The Island of Oahu, on which Honolulu sprawls, has a density greater than New Jersey, the most densely populated state.

[5] The nominal (not adjusted for inflation) exvessel revenue from commercial fishing was $3.9 million in 1970, $13.0 million when adjusted for inflation to 1990 consumer price levels.

[6] We exclude the lucrative ocean recreation sector, as well as the aquarium fish market and dive shops since these rely primarily on inshore and reef resources.

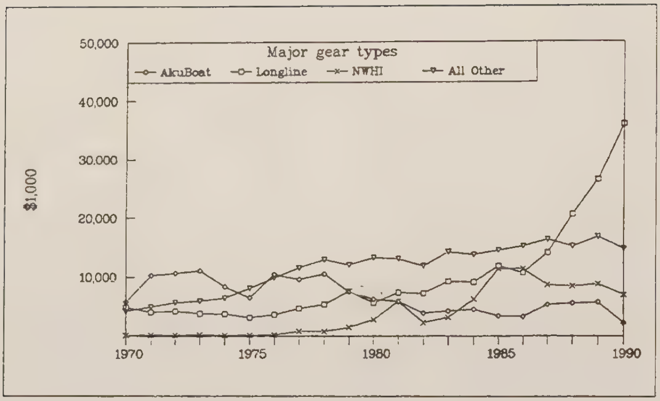

Figure 1.—NMFS estimates of commercial fishing revenue, adjusted for inflation, by major fleet components, 1970–92.

tion. The State of Hawaii commercial fishing license is quite inexpensive, and enforcement of its requirements is limited. A survey in 1984 found that 27% of small boat[7] owners sold a portion of their catch and 17% sold at least half their catch (Skillman and Louie[8]). Further study by Meyer[9] found that 35% of small boat catches were sold on the market and 13% were sold "off" the market, while 23% were retained for home consumption and 21% were given away to family and friends.

The overall level of recreational and subsistence fishing activity is difficult to assess. Meyer[9] estimates that the total catch by small boat fishermen (including some commercial landings) in 1985 was approximately 21 million pounds, of which 10 million pounds were sold. These are substantial numbers for Hawaii, when the recorded commercial fish landings by the small boat fleets was 5 million pounds in 1985.[10] The NMFS Marine Recreational Fishing Statistical Survey (MRFSS) which has served as the basic yardstick for recreational fishing landings (in weight and number, not value) across the mainland U.S. has not been conducted in Hawaii since 1981, and the results from the 1979–81 survey in Hawaii were not published. However, the unpublished MRFSS estimates suggest the volume of small-boat noncommercial marine landings in Hawaii was roughly 9 million pounds a year in that time period.[11] Assuming some positive relationship between small-boat commercial and noncommercial volume, there is no evidence from small-boat commercial landings in the late 1980's to suggest any dramatic change in the relative volume of the noncommercial sector. Furthermore, in a recent study reported by Hamm and Lum[12], recreational and subsistence landings (i.e., fish landed but not for sale) for the Island of Oahu amounted to 1.9 million pounds, based on a year-long small-boat survey. This amounted to 59% of the landed weight by these vessels (which excluded the charter boat fleet operating out of the Port of Honolulu and other larger commercial trolling vessels).

The monetary value of recreational and subsistence landings is even more difficult to assess, and comparison between the monetary value of recreational landings and commercial landings is a complex theoretical, indeed philosophical, issue. Meyer[9] estimated that the market value of the fish sold by recreational and subsistence fishermen was approximately $30 million (adjusted for inflation to 1990 price levels). However, the hedonic (or nonmarket) value of the recreational fishing experience was estimated at $335 million (inflation-adjusted) from direct expenditures on small-boat recreational and subsistence fishing of $33 million (inflation-adjusted). Since there are complex personal motivations for recreational and subsistence fishing, it is difficult to assess how much of this value should be associated with landing the fish, per se, and how much to other motivations.

In terms of participation, Skillman and Louie[8] estimated that there were at least 5,000 small boats actively used for fishing in Hawaii. The State of Hawaii recorded 3,500 commercial fishing licenses for fiscal year 1989, but this included licenses for crews on large-scale commercial fishing vessels as well as for small-boat fishermen. The state registers 1,100 vessels as commercial fishing boats (1989), but this excludes the larger vessels (documented by the U.S. Coast Guard), and choice of registration categories is somewhat dependent on tax status.

Figures on the level of recreational fishing activity in Hawaii are not entirely consistent. The MRFSS estimated the number of boat fishing trips in 1979–81 at 0.5 million annually. However, this amounts to over 1,350 trips per day, which seems excessive. Meyer[9] estimated that the average participation by small-boat fishermen was 38 trips per year, which would lead to an estimated 13,200 people who participated in small boat fishing in the mid-1980's. This seems like a generous number of trips per year (as an overall average) and a conservative number of actual participants. Until a comprehensive survey is conducted, these figures will remain elusive.

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[7] "Small boat" is a ubiquitous term referring primarily to troll, handline, and dive fishing vessels under 45 feet in length overall.

[8] R. A. Skillman and D. K. H. Louie. 1984. Inventory of U.S. vessels in the central and western Pacific: Phase 2—verification and classification. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-84-12, 21 p.

[9] Meyer Resources Inc. [P.A. Meyer]. 1987. A report on resident fishing in the Hawaiian islands (a project to determine the economic value of recreational fishing in Hawaii). U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-87-8C, 74 p.

[10] Unfortunately there is believed to be substantial underreporting in the state data. The extent of this underreporting for small boats is unknown.

[11] There was tremendous year-to-year variation in the estimates provided by the MRFSS survey which is primarily attributable to variation in number of fish landed and by average weight of fish (a composite of species composition and average weight per species). Clearly there were some substantial estimation problems with this survey approach, but the estimates probably indicate the relevant range of these fisheries.

[12] D. C. Hamm and H. K. Lum. 1992. Preliminary results of the Hawaii small-boat fisheries survey. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab, Southwest Fish. Sci. Cent. Admin. Rep. H-92-08, 35 p.

The value of fishing for subsistence by contemporary native Hawaiians and others has also not been calculated, but it is known to be an important component of some communities, particularly rural communities. Fish also have played an important cultural role. Iversen et al., in a study of anthropological sources, noted:

"There is abundant historical and archaeological evidence for the social and religious importance of bottomfish, aku (skipjack tuna), and sharks in traditional Hawaiian culture . . . . At the family level, sharks and aku were often conceived as 'aumakua — family or personal gods. The boundary between the supernatural world of these personal gods and the natural world of the Hawaiian people was not sharply defined" (Iversen et al.[13]).

For this paper I will not attempt to place a monetary-value estimate on subsistence fishing (separate from that identified above by Meyer[9]), except to acknowledge its importance.

Finally, Samples et al.[14] and Samples and Schug[15] estimated that the direct market value of charter boat fishing (i.e., the fees paid by patrons) was $8.5 million (inflation-adjusted) annually. At that time the charter boat fleet consisted of approximately 120 boats which took 75,000 trips annually. The charter boat fleet is understood to have grown fairly substantially over the past decade, particularly on the neighbor islands and in rural Oahu.

There is no direct comparison between the ex-vessel value of commercial fishing landings and the direct revenues of charter boat fishing, on the one hand, and the expenditures and hedonic values of recreational and subsistence fishing, on the other hand. Furthermore, there is substantial overlap in the estimates of landings by the small-boat fleets. However, a rough estimate of the direct input costs for all types of fishing combined would be $100 million[16]. Table 1 presents estimates of landings (pounds) for both sectors and dollar values for the commercial sector, including the seafood markets.

Only for commercial fishing can we estimate long-term trends in economic values. These appear in Figures 2 and 3. Inflation-adjusted ex-vessel revenue increased almost fourfold from 1970 to 1990, with dramatic increases in the past five years (threefold) owing to the

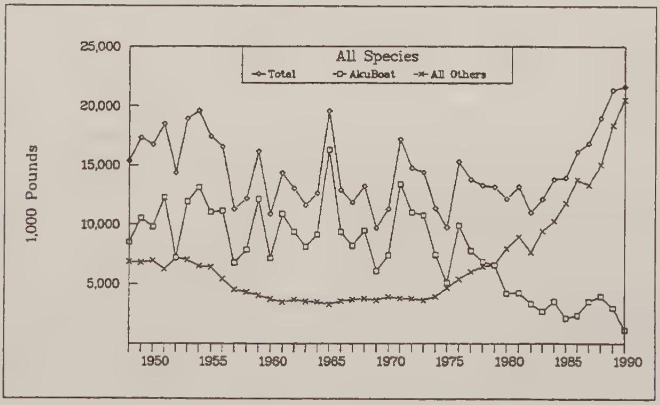

Figure 2.—NMFS estimates of commercial fishing landings, 1948–91.

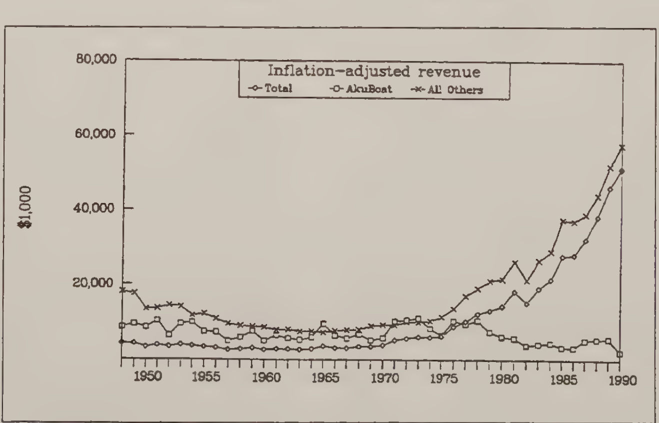

Figure 3.—NMFS estimates of commercial fishing revenue, adjusted for inflation, 1948–90.

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[13] R. Iversen, T. Dye, and L. M. B. Paul. 1989. Rights of native Hawaiian fishermen with specific regard to harvesting bottomfish in the Northwestern Hawaiian Islands and with regard to harvesting bottomfish, crustaceans, precious corals, and open-ocean fish in offshore areas surrounding the entire Hawaiian island chain. A report prepared for the Western Pacific Regional Fishery Management Council. Honolulu, Hawaii.

[14] K. C. Samples, J. N. Kusakabe, and J. T. Sproul. 1984. A description and economic appraisal of charter boat fishing in Hawaii. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-84- 6C, 130 p.

[15] K. C. Samples and D. M. Schug. 1985. Charter fishing patrons in Hawaii: a study of their demographics, motivations, expenditures and fishing values. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-85-8C, 95 p.

[16] Data on charter boat and recreational costs taken from Samples (1984, 1985), and the unpublished MRFSS for 1979-81. Commercial fishing costs were estimated to be equal to commercial fishing ex-vessel revenue.

Table 1.—NMFS estimates[1] of Hawaii fishery components, 1990. MHI = Main Hawaiian Islands; NWHI = Northwestern Hawaiian Islands.

Hawaii seafood supply and market,
1990 wholesale purchase level
NMFS estimates
(1,000's)

| Source of supply | Pounds | Dollars |
|---|---|---|
| Commercial fishing[2] | 21,000 | 50,400 |
| Recreational fishing[3] | 9,200 | |
| Hawaii fishery | 30,200 | 50,400 |
| Foreign imports[4] | 15,600 | 29,800 |
| U.S. mainland "imports"[5] | 24,300 | 46,500 |
| Export (foreign and U.S. mainland)[6] | 3,400 | 8,200 |
| Hawaii consumption[7] | 66,700 | |
| Hawaii market (commercial)[8] | 57,500 | 118,500 |

Hawaii commercial fisheries,
1990 NMFS estimates based on logbooks and
shoreside monitoring
NMFS estimates

| Fleet | Pounds caught | Pounds sold | Dollar |
|---|---|---|---|
| Longline | 13,090 | 12,200 | 28,800 |
| MHI troll-hand | 4,460 | 4,050 | 6,980 |
| Aku boat | 1,005 | 1,005 | 1,838 |
| MHI bottomfish | 830 | 810 | 3,300 |
| NWHI bottomfish | 420 | 400 | 1,070 |
| NWHI lobster | 949 | 949 | 4,887 |
| Other | 1,700 | 1,594 | 3,513 |
| Total | 22,454 | 21,008 | 50,388 |

[1] Honolulu Laboratory, National Marine Fisheries Service, Fishery Management Research Program.

[2] Hawaii commercial fishing: Domestic landings estimated by detailed NMFS logbooks and shoreside sampling, augmented by available State of Hawaii data for nonsampled fisheries.

[3] Recreational: Volume estimated in 1981 by NMFS Marine Recreational Fishing Statistical Survey.

[4] Foreign imports: volume (pounds) recorded by U.S. Food & Drug Administration monitoring; revenue estimated from Honolulu market prices by NMFS.

[5] U.S. mainland "imports": Volume and revenue estimated as proportion of Foreign imports using raising factors calculated from 1981 NMFS seafood market survey in Hawaii.

[6] Exports: Estimated from domestic landings of lobster, bottomfish, swordfish, and bigeye and yellowfin tuna.

[7] Hawaii consumption: Hawaii fishery + Imports – Exports.

[8] Hawaii market: Hawaii consumption – Recreational.

growth of the domestic longline fishing fleet. With a change in species and product composition from cannery tuna (34% of landings in 1980) to highly valued species (frozen lobster tails and fresh tunas, pelagics, and bottomfish), the inflation-adjusted price of fish in Hawaii also has risen dramatically, doubling from 1970 to 1990.

While it appears that some substantial profits have been made by some highliner sectors of the fishing fleet for short periods of time (e.g., the NWHI lobster fishery in the mid-1980's and the more technologically advanced swordfish boats in recent years), like most fisheries, Hawaii's commercial fishing sector provides employment and income more than an independent source of wealth. Many fisheries are characterized by limited profitability and declining incomes, and participation in commercial fisheries other than longline has probably been stable or declining (and there is a moratorium on entry into the longline fishery and the NWHI bottomfish and lobster fisheries). The seafood marketing sector may have a more stable profit-basis, but its competitiveness also suggests that capital income is relatively limited. This makes the public policy issues of fisheries management and development much more pointed than might be believed.

### Fishery Development

Fisheries development economics is a difficult blend of industry economics and the bioeconomics of fisheries management. Some of these problems have been considered in a planning context (Pooley[17]) which suggests that an interactive approach to fisheries development and management may be a more fruitful means for long-term sustainable development. However, most of the fisheries development work in Hawaii has been more traditional in its orientation, and there was relatively little conceptual work investigating the framework of fisheries development (Pooley[18]).

Throughout the late 1960's and the 1970's, fishery development was the predominant fisheries theme in Hawaii. The Pacific Tuna Development Foundation (PTDF)[19] was a joint State/Territory-Federal-industry body which initiated development projects throughout the Pacific, from advanced purse seine techniques which led to the initial movement of the U.S. tuna fleet from southern California to the western Pacific (primarily Papua New Guinea), to small-scale development activities such as teaching handline fishing techniques and building new boat launching ramps. The State of Hawaii through its Department of Land & Natural Resources sponsored the Hawaii Fishery Development Plan in 1979 (Hawaii Department of Land & Natural Resources[20]) which proposed a multi-million-dollar program of capital improvements and development projects aimed at establishing Hawaii as a base for distant water commercial fishing[21] and reinvigorating local fisheries[22]. Much of the NMFS research during this period was also directed toward fisheries development, including the tripartite study of the essentially uninhabited Northwestern Hawaiian Islands (NWHI) in the late 1970's (Grigg and Pfund, 1980). This study identified important lobster fishing grounds which at one point grew to be Hawaii's most lucrative single fishery ($6 million ex-vessel revenue in 1989).

Two important exogenous changes altered the climate for Hawaii's commercial fisheries during this period. In the mid-1970's, the increase in frequent neighbor island jet flights made possible the expansion of the domestic market for neighbor island fresh fish to Honolulu. This assisted the development of the neighbor island handline tuna and bottomfish fisheries. Furthermore, with the tremendous expansion of tourism and jumbo jet traffic between Hawaii and the mainland U.S. and between Hawaii and Japan, fresh fish from Hawaii gained new adherents and easier access to these external markets. This has been particularly true of the longline fishery, which reached its nadir in the late 1970's and which expanded steadily through the 1980's until the discovery of the swordfish fishery, at which point longlining exploded in volume. The closure of the Honolulu tuna cannery in 1984, coincident with worldwide changes in the structure of the U.S. tuna industry, reduced the basic infrastructure available for the commercial fishery for a number of years and also changed the low end of the tuna market (with increased supplies of fresh skipjack tuna competing with yellowfin tuna caught by handline vessels). No substantial alternative market has been developed for skipjack tuna, despite marketing assistance from two state agencies, the aku boat fleet has declined substantially, and the skipjack resource is essentially untapped around Hawaii.

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[17] S. G. Pooley. 1989. The role of government planning and economic analysis in the development of the private fisheries sector. Southwest Fisheries Center, Honolulu Laboratory manuscript MRF-003-90H, paper contributed to the International Symposium on Agriculture and Fisheries Development in Oman, Muscat, Oman.

[18] S. G. Pooley. 1985. The hopelessness of the invisible hand: small versus large fishing vessels in Hawaii. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-85-02, 16 p.

[19] Later renamed the Pacific Fishery Development Foundation.

[20] Hawaii Dep. of Land and Natural Resour. 1979. Hawaii Fisheries Development Plan. Dep. of Land and Natural Resources. State of Hawaii, Honolulu, Hawaii.

[21] Such as domestic purse seining (C. D. MacDonald and J. A. Mapes, 1985. Hawaii as a base for tuna purse seining operations. State of Hawaii, Dep. Planning and Econ. Develop., Honolulu, Hawaii).

[22] A parallel effort was made to develop onshore aquaculture (Hawaii Dep. Business and Economic Development, 1978), and despite a number of business failures, the wholesale value of aquaculture products produced in Hawaii was $9 million in 1990 (Corbin, 1992).

State of Hawaii fishery development activities continued throughout the 1980's[23], although the emphasis began to shift to "recreational" development (such as the deployment of fish aggregating devices [FAD's]) and to value-added seafood marketing (MacDonald et al., 1991). NMFS fishery development activity was increasingly directed through the Saltonstall-Kennedy grant process, and many of these funds were directed to other U.S.-associated areas in the western Pacific such as American Samoa, Guam, and the Northern Mariana Islands. The Saltonstall-Kennedy grant process also represented a privatization of development efforts in Hawaii, where most projects were carried out by individual fishing and seafood marketing companies.

### Economic Research

Hudgins[24] surveyed economic research to date in Hawaii. Since then there has been a suite of studies directed toward fisheries management issues and seafood marketing. A substantial amount of this research has been funded by the Southwest Fisheries Science Center's regional economics program (Pooley et al.[25]). The following is a précis of economic research in which the Honolulu Laboratory was the principal investigator or a major collaborator.

Economic research directed toward fisheries management began with attempts to estimate the value of the recreational billfish fishery (Adams[26]) using household production models. An alternative methodology, primarily travel cost and contingent valuation, was attempted by Samples and SMS Research, Inc.[27] and Meyer[9], but funds have never been adequate to conduct full-scale socioeconomic surveys of the recreational and subsistence fisheries in Hawaii.

The most applied set of studies, however, has concentrated on detailed cost-earnings profiles of various fleets. Most productive of these studies was the analysis of the Northwestern Hawaiian Islands (NWHI) lobster fleet. Clarke and Pooley (1988) reported a detailed breakdown of lobster fishing economic profiles by class of vessel. Samples and Sproul[28, 29] and Gates and Samples[30], in work funded by the Western Pacific Regional Fishery Management Council, undertook a preliminary investigation of management alternatives for the NWHI lobster fishery. This was followed by a detailed bioeconomic model of the fishery by Clarke et al. (1992) which identified the relationship between the lobster resource and fleet dynamics.

In 1979–81, NMFS conducted some broad research surveys of the Hawaii seafood markets (NMFS[31]) which attempted to identify the important market channels (Cooper and Pooley[32, 33]). Further studies were conducted on the nature of competition in the seafood market (Adams[34], Pooley[35]). These studies generally concluded that the existence of auction markets and a high level of competition between fresh and frozen food distributors had been beneficial for market development in Hawaii. However, there has been little follow-up to the initial surveys in the subsequent ten years. Research on market dynamics has continued, however, with data derived from systematic monitoring of the primary wholesale markets. Whereas results on the dynamics of the bottomfish market showed a strong relationship between quantity supplied and price, thus identifying the demand function (Pooley, 1987a), results from the more wide-ranging tuna markets were less robust because of either inadequacies in the data or substantial discontinuities in the market (Pooley[36, 37]). Work was also conducted by the Council in collaboration with NMFS on the marketing dynamics of the lobster fishery (Samples and Gates[38]).

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[23] Including an update of the fishery development plan (State of Hawaii, 1986) and the Hawaii Ocean Resources Management Plan (Hawaii Ocean and Marine Resources Council, 1991. Hawaii Ocean Resources Management Plan. Hawaii Dep. Business and Economic Development, Honolulu, Hawaii.).

[24] L. L. Hudgins. 1980. Economic analysis of Hawaii fisheries: a survey. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-80-07, 8 p.

[25] S. G. Pooley, S. F. Herrick, D. E. Squires, C. J. Thomsen, and G. W. Silverthorne. 1991. Southwest Fisheries Science Center and Southwest Region economics research plan, 1990-95. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Sci. Cent. Admin. Rep. H-91-07, 20 p.

[26] M. F. Adams. 1978. Alternative estimate of net economic benefits for billfish-tuna recreational commercial fishermen in Kailua-Kona, Hawaii. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-78-18, 10 p.

[27] K. C. Samples and SMS Research, Inc. 1983. Experimental valuation of recreational fishing in Hawaii. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-83-13C, 42 p.

[28] K. C. Samples and J. T. Sproul. 1987. Potential gains in fleet profitability from limiting entry into the Northwestern Hawaiian Island commercial lobster trap fishery. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-87- 17C, 30 p.

[29] K. C. Samples and J. T. Sproul. 1988. An economic appraisal of effort management alternatives for the Northwestern Hawaiian Islands commercial lobster fishery. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-88-12C.

[30] P. D. Gates and K. C. Samples. 1986. Dynamics of fleet composition and vessel fishing patterns in the Northwestern Hawaiian Islands commercial lobster fishery: 1983-86. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-86-17C, 32 p.

[31] National Marine Fisheries Service. 1982. Preliminary results of a survey of wholesale fish dealers in Hawaii. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-82-14, 17 p.

[32] J. C. Cooper and S. G. Pooley. 1982. Total seafood volume in Hawaii's wholesale fish markets. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-82-15, 12 p.

[33] J. C. Cooper and S. G. Pooley. 1983. Characteristics of Hawaii's wholesale seafood market. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-83-22, 33 p.

[34] M. F. Adams. 1981. Competition and market structure in the Hawaii fish industry. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-81-05, 20 p.

[35] S. G. Pooley. 1986. Competitive markets and bilateral exchange: the wholesale seafood market in Hawaii. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-86-08, 14 p.

Economic research with a development slant was conducted on the future of the Hawaii skipjack tuna cannery which closed in 1984. NMFS sponsored an industry and academic workshop on factors affecting the supply and market of skipjack tuna (Boggs and Pooley[39], 1987; Pooley, 1987b). This work supplemented earlier research on the supply function for domestic tuna production in Hawaii (Hudgins, 1980) and subsequent research on the future for tuna fisheries in the western Pacific (Hudgins and Pooley, 1987). The gist of the workshop was that while a substantial tuna resource (primarily skipjack tuna) existed which could be exploited, the dynamics of the international canned tuna market would probably preclude reestablishment of the pole-and-line aku fishery in Hawaii for the foreseeable future (King[40], 1987). Emphasis has instead been on export of fresh bigeye and yellowfin tuna. Research was also conducted on the nature of the skipjack tuna as a discrete economic product, with identification of price vectors based on the size of fish (Hudgins[41], 1987), and there was marketing research conducted on extending the shelf-life of skipjack tuna (Hawaii Department of Business and Economic Development, 1989). Finally, there is an additional economic value of longline fishing to Hawaii, but this is from the port visits of foreign fishing and reefer vessels which operate throughout the mid-Pacific region (outside the U.S. EEZ's). Hudgins and Iversen[42] estimate the value of these visits at $46 million based on 2,500 port calls.

Finally, several collaborative economic studies were carried out by NMFS on behalf of the Corps of Engineers concerning small-boat fishing from the islands of Hawaii (Pooley[43]), Maui (Pooley[44]) and Oahu (Pooley[45]) These studies emphasized applying prototypical cost-earnings results from each fishery to estimate the net economic benefits of alternative fishery development schemes[46].

## Fishery Management

Most of Hawaii's offshore marine fisheries are now under some form of Federal regulation through the Western Pacific Regional Fishery Management Council (Council). The basic premise of management under the Council for the NWHI lobster fishery and for the precious coral fishery has been to avoid biological overfishing. For the NWHI bottomfish fishery, avoidance of economic overfishing has been the primary motivation. In the MHI bottomfish fishery, primary concern has been on biological overfishing. Finally, the pelagic fishery (troll, handline, and longline gears used for catching tunas, billfish, and other ocean-dwelling pelagics) has been regulated essentially to avoid gear conflicts and other negative interactions between the growing longline fleet (targeting swordfish and tuna) and the smaller-scale troll and handline fleets (targeting tunas and billfish) (Pooley, 1990). However, the longline fleet was also excluded from areas around the NWHI to avoid interaction with endangered species, in particular the Hawaiian monk seal.

Despite the detailed cost-earnings and bioeconomic modeling of the NWHI lobster fishery, the limited entry program for NWHI lobster which was initiated in 1991 was based more on pragmatic grounds than on economic research per se. The limited entry program for bottomfishing in the NWHI was supported more directly by Council economic research in collaboration with NMFS (Meyer[9]) which attempted to identify the kinds of constraints facing the domestic fishing fleet. This work was not fully developed in terms of quantifying the pa-

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[36] S. G. Pooley. 1990. Pelagic species prices in 1987-88. Southwest Fisheries Center, Honolulu Laboratory manuscript MRF-002-90H.

[37] S. G. Pooley. 1991. Revised market analysis: Hawaii yellowfin tuna. Southwest Fisheries Science Center, Honolulu Laboratory manuscript 003-091H-MRF.

[38] K. C. Samples and P. D. Gates. 1987. Market situation and outlook for Northwestern Hawaiian Islands spiny and slipper lobsters. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-87-4C, 33 p.

[39] C. H. Boggs and S. G. Pooley. 1987. Strategic planning for Hawaii's aku industry. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-87-01, 15 p.

[40] D. M. King. 1986. Global tuna markets and Hawaii aku. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-86-12C, 15 p.

[41] L. L. Hudgins. 1986. Economic issues of the size distribution of fish caught in the Hawaiian skipjack tuna fishery, 1964-82. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-86-14, 16 p.

[42] L. L. Hudgins and R. T. B. Iversen. 1990. Foreign flag fishing vessel expenditures in the Port of Honolulu, 1986–88. Report prepared for the State of Hawaii, Dep. Business, Economic Development and Tourism, Honolulu, Hawaii.

[43] East Hawaii commercial fishing mooring/launching facility project: economic and resources analysis. Southwest Fisheries Sci. Center, Honolulu Laboratory manuscript MRF-006-89H, report prepared for the U.S. Army Engineer Division, Pacific Ocean.

[44] Kahului small fishing boat facility: alternative net benefit estimates. Southwest Fisheries Sci. Center, Honolulu Laboratory manuscript MRF-004-89H, report prepared for the U.S. Army Engineer Division, Pacific Ocean.

[45] Report on Oahu small boat harbor fishery potential—Heeia Kea and Maunalua Bay. Southwest Fisheries Sci. Center, Honolulu Laboratory manuscript MRF-005-89H, report prepared for the U.S. Army Engineer Division, Pacific Ocean.

[46] Similar survey work was conducted for American Samoa, Guam, and the Northern Mariana Islands in cooperation with the island fishery agencies (L. D. Kasaoka. 1989. Summary of small boat economic surveys from American Samoa, Guam, and the Northern Mariana Islands. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-89-4C, 47 p.). However development of cost-earnings profiles was not completed due to lack of research resources.

rameters, but Pooley and Kawamoto[47] developed a series of cost-earnings profiles of the NWHI bottom fishing fleet which have been used in Council determinations on potential new entry into the fishery.

The limited entry regimes for NWHI bottomfish and lobster are both based on break-even levels of fishing effort at maximum sustainable yield. However, there has been relatively little interest in actually optimizing these fisheries. Where the biological dynamics of these fisheries are not well understood, and where the economics of fleet behavior between fisheries are quite fluid, these regimes may be considered quite appropriately as second-best optima under the circumstances.

Attempts at constructing linear programming models of the NWHI fishery (both as a directed bottomfish fishery and as a multipurpose fishery) were not particularly successful, but some experiments have been undertaken to model the components of fishing vessel operator behavior (Miklius and Leung[48]). This represents a novel approach to modeling decision processes and is based on detailed examination of vessel owner and captain incentives.

Although a considerable part of the pelagic fishery management problem revolves around allocation issues between segments of the fishery, information for fully developed economic models has been inadequate. The economic research mentioned in the description of Hawaii's recreational and subsistence fisheries, as well as the collaborative Corps of Engineers surveys, has been useful for fishery management purposes. Qualitative information was provided in the regulatory impact analysis of one amendment to the Pelagic Species Fishery Management Plan[49], but considerably more research is required.

Finally, although almost all of this research has revolved around Hawaii and has been directly economic in orientation, other pieces of social science research have been quite productive. Perhaps the most promising was the application of political bargaining models to the potential of management of South Pacific albacore (Schug, In press). This model looked at the constituent elements to successful negotiations and evaluated the conditions in that fishery during the conflict over drift-net fishing. The work is being extended to the current era when drift-net fishing has ceased.

### Central Economic Issues

From one perspective, the central economic issues in Hawaii's marine fisheries are fairly simple. Because of the geographical isolation of Hawaii from other U.S. fishing fleets and because of the vastness of the central and western Pacific, as well as the distances and costs involved in fishing the NWHI, the large-scale commercial fisheries have tended to "manage themselves" to a certain extent. The regulatory structures at both a biological and economic level have been relatively simple, and interactions between fisheries are limited. On the other hand, since most of these fisheries have just completed their development stage, relatively little information is available on them, and both formal and informal management institutions, including associations of fishing participants, are even younger. Therefore each regulatory action is taken with a high degree of uncertainty concerning its effect on the participants in the fisheries and those associated with the fisheries[50].

A good example has been the recent closure of waters around the main Hawaiian Islands to longline fishing. The closures were designed to reduce gear interactions between the longline fleet on the one hand and troll and handline boats on the other, while still allowing the longline fleet access to the remainder of the waters around Hawaii. At the time, a considerable portion of the fleet was traveling as much as 1,200 miles from Honolulu, but two segments of the longline fleet were adversely affected. It was anticipated that the smaller wooden and fiberglass longline sampans would be affected, and provision to allow them exemptions to fish in their customary waters inside the closure was recommended.[51] It was not anticipated that a substantial portion of the remaining portion of the fleet, as many as 30–40 modern longline vessels, would choose to tie-up rather than fish outside the closure area. (The reasons for this are not yet clear.) Furthermore, although there was a presumption that the closures would be a de facto allocation in favor of the commercial troll and handline boats, their landings apparently did not rise during the period. The resulting impact of reduced landings on the local seafood market for tuna and other pelagics was substantial during the summer and fall of 1991, and a number of dealers also indicated economic hardship as a result of the closures.

This leads to the central economic issue in Hawaii's marine fisheries: the allocation of uncertain quantities of fish (primarily tunas and pelagics but also bottomfish) between the larger-scale commercial fishing fleets and the smaller-scale commercial, part-time commercial, subsistence, and recreational fishing boats. The subject may be intensified by native Hawaiian claims to preference in some of these fisheries (Iversen et al.[13]), but research on these issues is primarily in the purview of the Council and the State of Hawaii's Office of Hawaiian Affairs.

Biologically, a commercially caught fish is pretty much the same as a recreationally caught fish in Hawaii, although there are some size composition differences. U.S. fishery management history tended to favor domestic commercial fisheries until the late 1980's, with the pendulum now tending to swing more towards conservation and towards recreational and small-scale commercial interests. That has certainly been the case in Hawaii's pelagic fishery interaction issue. On the other hand, in the MHI bottomfish case, conservation has clashed substantially with recreational, subsistence, and small-scale commercial interests, with a large presumption going toward access, rather than conservation.

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[47] S. G. Pooley and K. E. Kawamoto. 1990. Economic analysis of bottomfish fishing vessels operating in the Northwestern Hawaiian Islands, 1984-88. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Sci. Cent. Admin. Rep. H-90-13, 21 p.

[48] W. Miklius and P. S. Leung. 1990. Behavior modeling in the multi-fishery: an evaluation of alternative methods. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Sci. Cent. Admin. Rep. H-90-11C, 13 p.

[49] Proposed regulatory impact review: Amendment 4: Pelagic Fisheries FMP. Southwest Fisheries Science Center, Honolulu Laboratory manuscript 005-91H-MRF.

[50] This is true of many mainland U.S. fisheries as well. The difference is the very short time-series of information on which to base resource and economic assessments in Hawaii.

[51] As it turned out, only a few of these vessels met the stringent qualifying criteria.

From one point of view, the political pluralism of the MFCMA fishery management system is an appropriate balancing of these concerns. Not only are there representatives of different fishing interests on the Council, there is also direct representation from different levels of government. Furthermore, at least in Hawaii, there is relatively easy access to the Council process, including a quite vocal and frequently educational public hearing process. On the other hand, some people fear that the decision-making process has not had or used enough information on the relative benefits and costs to the various human components of the fisheries. Weighing the market value of a commercially caught fish in terms of its income and employment generating impact against the nonmarket value of a recreationally caught fish in terms of enjoyment and personal consumption is hard enough. This is made more difficult by monetized and nonmonetary "rights" to fishing access and the probability that reducing large-scale commercial fishing probably will not generate an equivalent volume of landings (in weight or numbers) through the alternative fisheries. Then, the question becomes one of evaluating the marginal impact of fishing regulations on multiple interest groups. Furthermore, as contentious as the marine fisheries issues have been, a much more contentious set of marine resource issues faces Hawaii legislators and resource managers: the alternative uses of the near-shore and coastal environment (Hawaii Ocean and Marine Resources Council[52]). In Hawaii, we are nowhere near making such determinations.

## Conclusion

What can economic and social science research contribute to the weighing of benefits and costs from development and conservation in Hawaii's marine fisheries? The answer to this question lies in the nature of the regulatory process.

Fisheries management, as codified by the MFCMA and various Federal rules, is a political process dominated by strategic bargaining on the part of its participating interest groups. As such, it is a classic example of political pluralism at the margin within tightly structured political boundaries and loosely structured economic and social systems. This political process contrasts strongly with three important presumptions in the MFCMA process:

1) Regulatory legalism,
2) Scientific rationalism, and
3) Laissez-faire economic ideology.

Clearly, in addition, there is a strong natural science presumption to issues of fisheries management, even though it is now commonplace to acknowledge that it is the people who participate in the fishery, from the harvesters to the dealers who are managed, not fish. Although participants in the fisheries management process know parts of this regulatory landscape, there is very little systematic knowledge of these basic contradictions.

Probably the most important potential contribution of social science research would be toward understanding the behavior of individuals and groups in the fishing community, particularly in terms of understanding changes in human behavior due to regulation (ex ante and contrapositive), endogenous changes in fishing technology, and exogenous events such as changes in alternative labor markets, changes in oil prices, or changes in ocean and coastal zone use. This requires a fact-based, micro approach to social science research, not abstract models of fishing behavior. Unfortunately, although this kind of research promises important contributions to fisheries management decisions, neither its time frame nor its research resource requirements correspond to the short-term agendas of fisheries management bodies.

In Hawaii this should suggest two new approaches. First, there should be a wider scope for fisheries economics research to include a range of marine resource use issues as well as coastal zone and environmental economic issues. Second, this research should include a wider collaboration between university, state, and Federal researchers in a number of agencies, and probably a greater explicit collaboration with fishing (and similar user group) communities in the conduct of economic research. These approaches would take substantial new research resources, but they remain trivial compared to the overall cost of natural science research in fisheries and the social opportunity costs of overharvesting.

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# Hawaii's Marine Fisheries: Some History, Long-term Trends, and Recent Developments

SAMUEL G. POOLEY

## Introduction

Recently Hawaii's commercial marine fishery has experienced a period of rapid growth and structural change, and its characteristics are quite different from what they were a decade ago. Some of these changes are the result of governmental and private-sector decisions on fishery development in Hawaii, but many have occurred because of increasingly competitive pressures, particularly as they have affected mainland U.S. commercial fishing fleets. Further changes are anticipated as diverse fishing interests (including both large-scale and small-scale commercial, indigenous, and recreational fishing interests, as well as nonconsumptive marine resource interests) are worked out in fishery, marine, and coastal zone management processes. This paper concentrates on the economic development of the offshore commercial fishery, and places somewhat greater emphasis on the large-scale fisheries. Biological and management features of Hawaii's marine fisheries are considered in other papers in this number (Mar. Fish. Rev. 55(2)).

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*ABSTRACT — This paper provides an overview of Hawaii's marine fisheries from 1948 to the present. After three decades of decline following a brief period of growth at the conclusion to World War II, Hawaii's commercial fisheries began a decade of sustained development in the 1980's. At the same time, fisheries management issues became more significant as different segments of the fishery came into more direct competition. This paper provides new estimates of commercial landings for the 1977–90 period, and summarizes limited information on recreational and subsistence fisheries in the 1980's. It also provides some historical context which may be useful in evaluating fishery development and management options.*

Hawaii's marine fisheries can be divided into three geographical areas (Fig. 1):

1) The inhabited main Hawaiian Islands (MHI), with their surrounding reefs and offshore banks (the island of Hawaii to Niihau and Kauai);

2) The Northwestern Hawaiian Islands (NWHI), a 1,200 mile string of basically uninhabited reefs, shoals, and islets ranging west northwest from the main Hawaiian Islands (i.e., west of Niihau and Kauai);

3) The mid-North Pacific Ocean, ranging from lat. 40°N to the Equator, and from long.145°W to long. 175°E.

Hawaii's fishing fleets can also be divided into three somewhat overlapping or interconnected segments:

1) Large-scale commercial fishing.

**Table 1.—List of common and scientific names of frequently caught commercial species in Hawaii.**

| Common name | Scientific name |
|---|---|
| Bottomfish | |
| Snappers | |
| Onaga | *Etelis coruscans* |
| Opakapaka | *Pristipomoides filamentosus* |
| Ehu | *E. carbunculus* |
| Kalekale | *P. seiboldii* |
| Gindai | *P. zonatus* |
| Uku | *Aprion virescens* |
| Lehi | *Aphareus rutilans* |
| Yellowtail kalekale | *P. auricilla* |
| Taape | *Lutjanus kasmira* |
| Grouper | |
| Hapuupuu | *Epinephelus quernus* |
| Jacks | |
| White ulua | *Caranx ignobilis* |
| Black ulua | *C. lugubris* |
| Butaguchi | *Pseudocaranx dentex* |
| Kahala | *Seriola dumerili* |
| Other | |
| Lobster | |
| Spiny | *Panulirus marginatus* |
| Slipper | *Scyllarides squammosus* |
| Pelagic Management Unit Species | |
| Blue marlin | *Makaira mazara* |
| Striped marlin | *Tetrapturus audax* |
| Broadbill swordfish | *Xiphias gladius* |
| Shortbill spearfish | *T. angustirostris* |
| Black marlin | *M. indica* |
| Indo-Pacific sailfish | *Istiophorus platypterus* |
| Mahimahi | *Coryphaena hippurus* |
| Ono (wahoo) | *Acanthocybium solandri* |
| Blue shark | *Prionace glauca* |
| Mako shark (short-fin) | *Isurus oxyrinchus* |
| Mako shark (long-fin) | *I. paucus* |
| Oceanic whitetip shark | *Carcharhinus longimanus* |
| Thresher shark | *Alopias superciliosus* |
| Tiger shark | *Galeocerdo cuvieri* |
| Tunas | |
| Bigeye Tuna | *Thunnus obesus* |
| Yellowfin tuna | *T. albacares* |
| Albacore | *T. alalunga* |
| Skipjack tuna (Aku) | *Katsuwonus pelamis* |
| Kawakawa | *Euthynnus affinis* |
| Frigate tunas | *Auxis* spp. |

Although termed "large-scale" in Hawaii, by mainland U.S. and foreign fishing fleet standards almost all the vessels in this segment would be considered small. Most "large-scale" commercial fishing vessels in Hawaii are less than 100 feet in overall length. These include the older aku boats (pole-and-line sampans[1] fishing for skipjack tuna[2]) (Table 1) and tuna longline sampans (also wooden but of a different design), as well as modern tuna and swordfish longline vessels, distant-wa-

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[1] The term "sampan" in Hawaii refers primarily to wooden-hulled fishing craft of a design introduced by Japanese fishermen in the early 1900's. The vessels range from 35 to 75 feet with a flared bow, a low stern, and a deep profile to maintain seaworthiness in Hawaii's rough waters.

[2] Hawaii common names for commercial marine fish and shellfish species are used throughout this paper. Scientific names and corresponding Hawaii, names are found in Table 1.

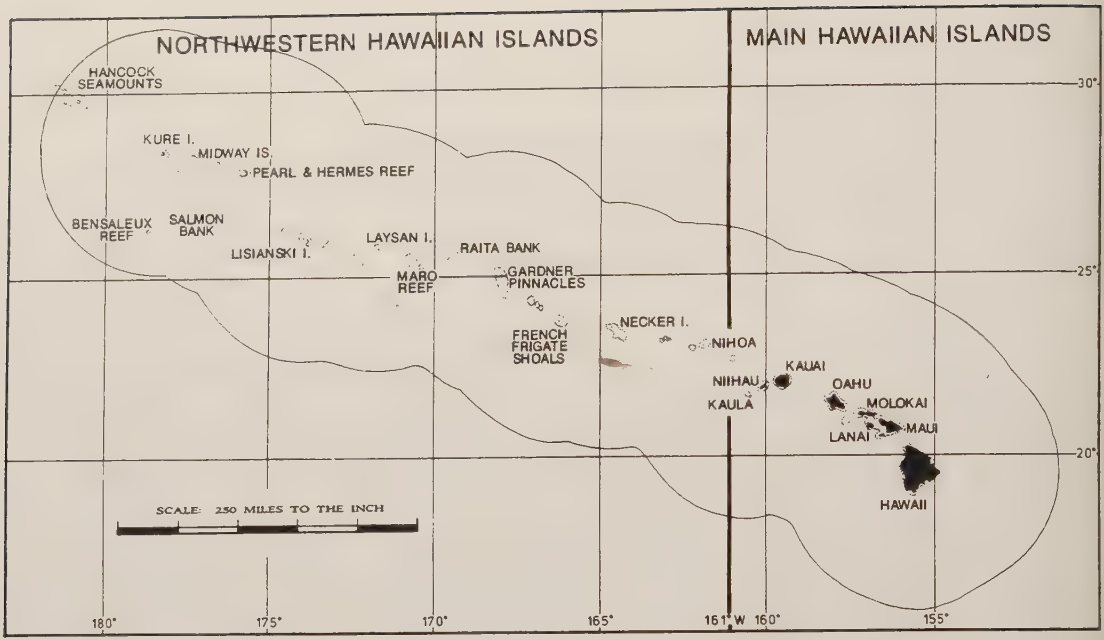
NORTHWESTERN HAWAIIAN ISLANDS
MAIN HAWAIIAN ISLANDS
HANCOCK SEAMOUNTS
KURE I.
MIDWAY IS.
PEARL & HERMES REEF
BENSALEUX REEF
SALMON BANK
LISIANSKI I.
LAYSAN I.
RAITA BANK
MARO REEF
GARDNER PINNACLES
FRENCH FRIGATE SHOALS
NECKER I.
NIHOA
KAUAI
NIIHAU
KAULA
OAHU
MOLOKAI
LANAI
MAUI
HAWAII
SCALE: 250 MILES TO THE INCH
30°
25°
20°
180°
175°
170°
165°
161° W
160°
155°

Figure 1.—Hawaii map, including NWHI.

ter albacore trollers, and multipurpose vessels which fish for bottomfish (deepwater snappers, groupers, and jacks) and spiny and slipper lobster in the NWHI. These vessels can operate as far as 1,000 nautical miles from Hawaii throughout the mid-North Pacific, and some span the South Pacific. Most operate within 200 miles of the MHI or within the NWHI.

2) Small-scale commercial fishing. The vessels in this segment include a wide variety of trailered and moored boats between 12 and 45 feet in length. These vessels primarily use trolling and handline techniques, although some traps and surrounding nets are used. The target species include tunas, billfish, mahimahi, ono (wahoo), bottomfish for the trollers and handliners; bottomfish, reef fish, and crustaceans for the trap vessels; and small midwater scads (known locally as akule and opelu) for the surrounding-net fishery. These vessels operate almost exclusively in the MHI.

3) Small-scale recreational, part-time commercial, and subsistence fishing. This segment includes the same kind of vessels as found in the small-scale commercial fleet, as well as some very small boats (including surf boards and sail boards), charter fishing boats and dive fishing boats. Although charter fishing is a commercial operation, its clients are oriented toward recreational opportunities and thus it is distinguished from commercial fishing. The target species for this segment of the fishery are more varied than those of the commercial segments, and include a variety of reef species, as well as the more familiar tunas, billfish, mahimahi and ono (wahoo), bottomfish, and crustaceans. The fishing methods used are also considerably more varied.

The issue of categorizing Hawaii's small-boat fisheries is a difficult one, and is discussed later in this paper. For the moment we would categorize this segment as one where the fishery has limited fishing power and its fishermen have mixed motivations in terms of fishing activity.

## Hawaii's Traditional Commercial Marine Fisheries

Shortly after Statehood, a U.S. Department of Interior, Bureau of Commercial Fisheries proposal labeled the Hawaii fishery as "dying" (Iversen[3]). Hawaii's major commercial fisheries had been dominated by traditional practices that reflected Hawaii's Japanese immigrant heritage and its impact on the local fishery and seafood markets. The predominant commercial fishery was aku (skipjack tuna), which was caught by a live-bait, pole-and-line, wooden sampan fleet, known as aku boats (Fig. 2), and which was landed primarily for canning. In 1960, over 60% of Hawaii's total recorded commercial fishery landings (by weight) was aku, and the percentage remained over 50% until 1970.

By the mid-1970's the number of aku boats and their companion sam-

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[3] R. T. B. Iversen, 45-626 Halekou Place, Kaneohe, HI 96744. Personal commun., 1991.

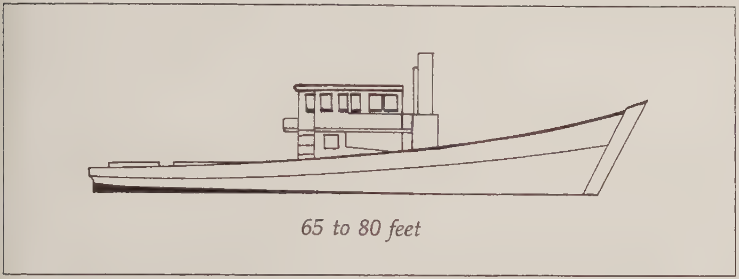

Figure 2.—Drawing of typical Hawaii aku (skipjack tuna pole-and-line) boat.

**Table 2.—Hawaii commercial fisheries, 1990. NMFS estimates based on logbooks and shoreside monitoring. MHI = main Hawaiian Islands; NWHI = Northwestern Hawaiian Islands.**

| Fleet | Weight (1,000 lb.) Caught | Weight (1,000 lb.) Sold | Thousand dollars |
|---|---|---|---|
| Longline | 13,090 | 12,200 | $28,800 |
| Troll and handline pelagics | 4,460 | 4,050 | 6,980 |
| Aku boat | 1,005 | 1,005 | 1,838 |
| MHI bottomfish | 830 | 810 | 3,300 |
| NWHI bottomfish | 420 | 400 | 1,070 |
| NWHI lobster | 949 | 949 | 4,887 |
| Other | 1,700 | 1,594 | 3,513 |
| Total | 22,454 | 21,008 | 50,388 |

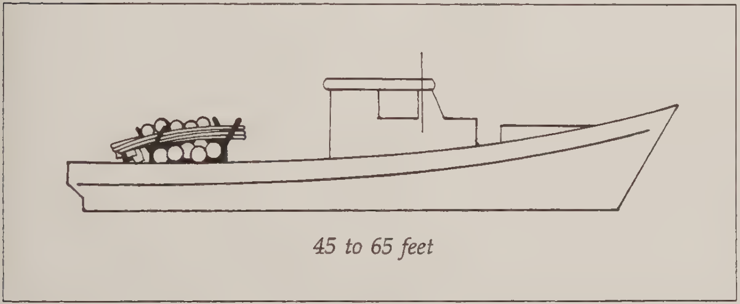

Figure 3.—Drawing of typical Hawaii flagline (longline sampan) boat.

pans, the longline tuna boats (known locally as flagline boats, Fig. 3), had decreased substantially, and the condition of many of the boats was poor. Fishing remained close to the main Hawaiian islands, although some older bottomfish boats fished the NWHI. Volume of fish in the fresh fish market had declined, and few improvements in marketing were apparent. Most fresh seafood appeared to be consumed in the home, and ethnic identification with particular species was very strong. Nearshore reef and schooling fish were still relatively abundant, but Hawaii's commercial fishery reached its nadir in 1975.[4]

Figures 4 and 5 provide estimates of Hawaii's long-term commercial fishing landings and revenue.[5] Revenues throughout this paper are inflation-adjusted values to a 1990 base year. Figures on landings and revenue for the period 1948–76 are based entirely on the Hawaii Division of Aquatic Resources (HDAR) commercial fishing landings reports. Figures for the period 1986–90 are based largely on NMFS estimates of Hawaii's commercial landings and on our own wholesale market monitoring program. The period 1977–85 is a combination of the HDAR data with NMFS estimates of particular gear types (longline and NWHI lobster).[6] Table 2 provides a breakdown of the NMFS data for 1990 by gear type.

Figure 4 differentiates the aku boat fishery (skipjack tuna) from the rest of the fishery (identified as "non-aku") because the aku fleet has been the source of most annual variation in landings. The average annual variation in detrended aku landings was 164% (compared with 27% for non-aku landings) in the period 1948–90.[7] Any analysis of the overall Hawaii commercial fishery over time must differentiate the overall trend from these fluctuations in the aku fishery.

Aku landings declined through the mid-1970's to the closing of the cannery in 1984, and then continued to fall through 1990. Aku landings fell as a percentage of total landings (by weight) from over 70% in the 1960's to less than 20% in the last five years of the 1980's, and to only 4.5% in 1990. However aku revenue has not fallen as appreciably because of the higher market price of fresh aku (compared with the cannery price in the pre-1985 period).

## Major Developments Since the Mid-1970's

The nature and value of Hawaii's present day fisheries and seafood industry have changed dramatically since the 1970's. The commercial fishery has more than doubled in inflation-adjusted ex-vessel value since 1970 to $50 million in 1990 and $60 million in 1991. The seafood market is probably worth over $100 million (including imported seafood), there is a $10-15 million char-

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[4] In terms of inflation-adjusted revenue. The lowest landings were in 1969 using NMFS estimates, but 1975 was the second lowest year.

[5] Estimates are required because official records of commercial fisheries landings were not comprehensive in some years during that period.

[6] Appendix A, available from the author, provides additional detail on the NMFS estimates for the period 1979-90, as well as time-series for individual gear types (aku boat, longline, NWHI lobster, NWHI bottomfish, main Hawaiian Islands, and other gears) from 1948 to 90.

[7] Detrending is a simple statistical procedure to remove the long-term change (growth or decline) in a time series. The resulting figures then reflect more accurately the shorter-term variation, in this case, the year-to-year variation, in the 1948 to 1990 time period.

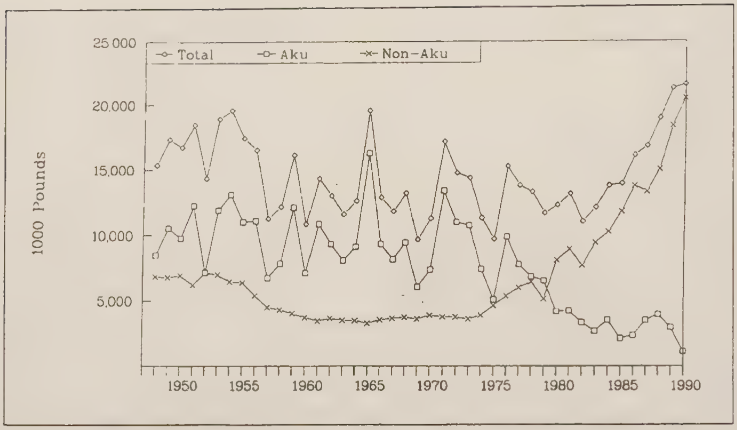

Figure 4.—Hawaii commercial fishery landings (pounds), 1948-90. NMFS estimates, total, aku (skipjack tuna), and all other species.

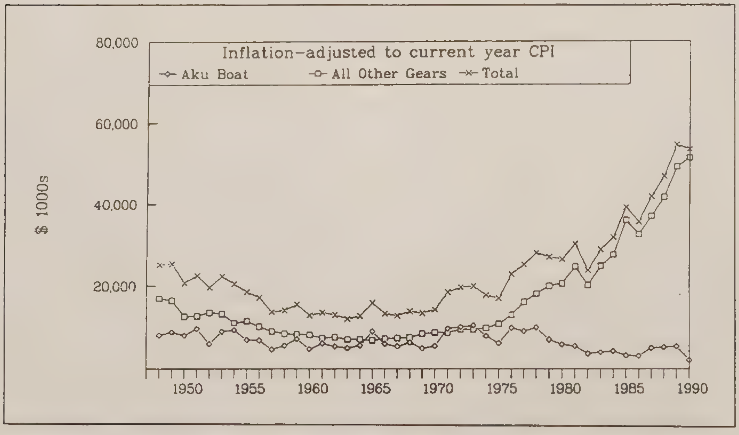

Figure 5.—Hawaii commercial fishery revenue, 1948-90. NMFS estimates, total, aku boat (pole-n-line skipjack tuna), and all other gears. Revenue adjusted for inflation to 1990 U.S. $ base.

ter boat industry, probably an equivalently valued tournament fishery, and there is a recreational and subsistence marine fishery with direct expenditures of $24 million.[8] Figure 6 displays our estimate of the Hawaii seafood market supply in 1990, with 20 million pounds ($50 million) from commercial fishing, 9 million pounds from recreational fishing, 15 million pounds ($30 million) from foreign imports, 24 million pounds ($45 million) from the mainland U.S., and 3.5 million pounds ($10 million) exported.[9]

Perhaps the most notable long-term trend in Hawaii's overall commercial fishery is the dramatic increase in inflation-adjusted ex-vessel revenue in the 1980's (Fig. 5). The increase in revenue (240%), which is reflected in the increased value of the marketing sector, is even greater than the increase in pounds landed (200%), although less than the increase in non-aku landings (300%). The increase in average aggregate price reflects a substantially growing demand, particularly in the restaurant and export (U.S. mainland and foreign) markets, more than matching the increased supply for most species during the period.

There are many elements to these recent changes in Hawaii's seafood industry. Perhaps the first harbinger of change was the arrival of albacore trollers from the west coast en route to newly discovered fishing grounds north of Midway Islands late in the 1970's. This caused a new perspective on the nature of Hawaii's role in the Pacific-wide fishery and led to some substantial changes on the Honolulu waterfront. Not the least of these changes was the technological demonstration effect of the mere presence of these distant-water, highly mobile vessels[10]. In 1985, there were 75 albacore trollers in the U.S. North Pacific fishery (Hawaii Division of Aquatic Resources, 1986). Landings peaked at 3.8 million pounds, but because of logistics, the closure of the Honolulu cannery, and the changing world tuna market, Hawaii did not become the tuna processing and transshipment center that was anticipated. Eventually less than 20 albacore vessels chose to make Honolulu their home port.

Also in the 1980's, the Northwestern Hawaiian Islands spiny lobster fishery began to bloom. The NWHI possess a large EEZ but have relatively limited fishing grounds for nonpelagic species. During a cooperative research effort of the NMFS, HDAR, University of Hawaii, and U.S. Fish and Wildlife Service in the 1970's (Grigg and Tanoue,

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[8] The definition and determination of "value" for recreational and subsistence fisheries is a complex methodological issue. Direct comparison of the expressed dollar values of commercial vs. recreational fisheries is generally not appropriate; see Edwards (1990) for a primer on these issues. Meyer (footnote 20) estimated the nonmarket value of small-boat noncommercial fishing in Hawaii at $200 million, using hedonic valuation methods, compared to actual direct expenditures of $24 million.

[9] Hawaii's seafood marketing sector is described in: J. C. Cooper and S. G. Pooley. 1982. Total seafood volume in Hawaii's wholesale fish markets. Southwest Fish. Cent. Admin. Rep.H-82-15, 12 p.; J. C. Cooper and S. G. Pooley. 1983. Characteristics of Hawaii's wholesale seafood market. Southwest Fish. Cent. Admin. Rep. H-83-22, 33 p.; W. K. Higuchi and S. G. Pooley. 1985. Hawaii's retail seafood volume. Southwest Fish. Cent. Admin. Rep. H-85-06, 16 p.; and MacDonald and Deese (1988).

[10] The demonstration effect relects indirect learning initiated by the presence of a new technology or methodology, usually introduced into a culture or a society from outside.

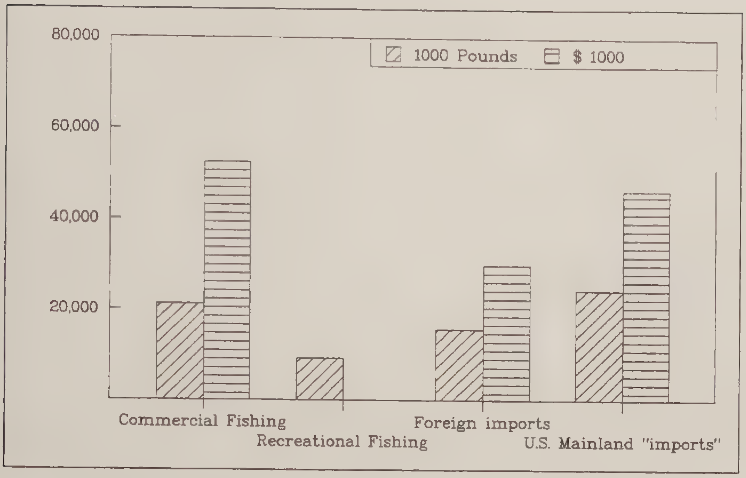

Figure 6.—Hawaii seafood market shares, 1990. NMFS estimates.

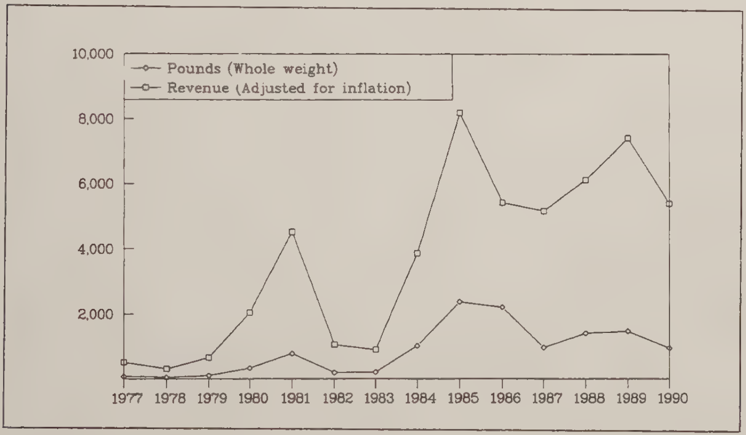

Figure 7.—NWHI lobster landings, pounds and revenue, 1977-90. NMFS estimates and figures. Revenue adjusted for inflation to 1990 U.S. $ base.

1984), scientists discovered substantial quantities of spiny lobster in the NWHI. By the mid-1980's, with the additional discovery of slipper lobster, NWHI lobster was one of Hawaii's largest fisheries in terms of ex-vessel revenue (Fig. 7). To develop the lobster fishery, new fishermen and new boats came to Hawaii, primarily from the Pacific Northwest (Fig. 8). Large vessels, some over 100 feet in length, with advanced technology freezing and processing equipment, entered the fishery. New traps were introduced from California which made fishing not only more efficient but also allowed the slipper lobster to be caught commercially.

Although the first lobsters were sold locally as a live product, soon almost all were produced as a frozen tail product and sold to mainland U.S. buyers. This was the first premium product of Hawaii's new commercial fisheries, with prices ranging up to $13.50 per pound for the tails. However, neither the albacore nor the lobster fishery changed the basic structure of the Hawaii fresh fish market.

The NWHI also proved to be a good location for bottom fishing (mechanized "handline" fishing for snappers, groupers, and jacks), which required a medium-scale modern fishing vessel (Fig. 9) similar to those used in the lobster and albacore fisheries. The expanding supply of pink and red snappers (opakapaka and onaga) locally made possible the expansion of the restaurant market by allowing a regular and consistent supply of relatively fresh fish (Fig. 10). At the same time, the restaurant market for fresh mahimahi also expanded, providing a new source of income for local trollers (Takenaka et al.[11]). Local wholesale dealers were able to promote fresh local mahimahi as a substitute for some of the large imports of frozen mahimahi. Since both bottom fish and mahimahi were landed fresh and sold primarily at the Honolulu auction, this marked an important change in the local fishery and reinvigorated the local fresh fish market.

With a much larger restaurant market in Honolulu, bottomfish fishermen from the main Hawaiian Islands were able to obtain premium prices for their considerably fresher catch, and thus were motivated to increase their landings (Fig. 11). Finally, some wholesale seafood dealers began sending opakapaka and mahimahi to the mainland, establishing a distinctively Hawaiian seafood presence linked to Hawaii's tourism market.

In the late 1970's and early 1980's the traditional Hawaiian tuna handline fisheries, known as ika shibi (Ikehara[12]) and palu ahi, revived owing to fuel-efficient small-scale vessels (Fig. 12). These fisheries, which targeted yellowfin and bigeye tuna (both known locally as ahi, along with albacore), were centered on the Big Island (Hawaii), but much of the product at the time was shipped to Honolulu for the restaurant market. This was a useful de-

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[11] B. Takenaka, L. Toricer, S. G. Pooley, and J. C. Cooper. 1984. Recent trends in the commercial fishery and marketing of mahimahi and ono in Hawaii. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-84-9, 20 p.

[12] W. Ikehara. 1981. A survey of the ika-shibi fishery in the state of Hawaii, 1980. U.S. Dep. Commer., NOAA, Natl. Mar.Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin Rep. H-82-4C, 11 p.

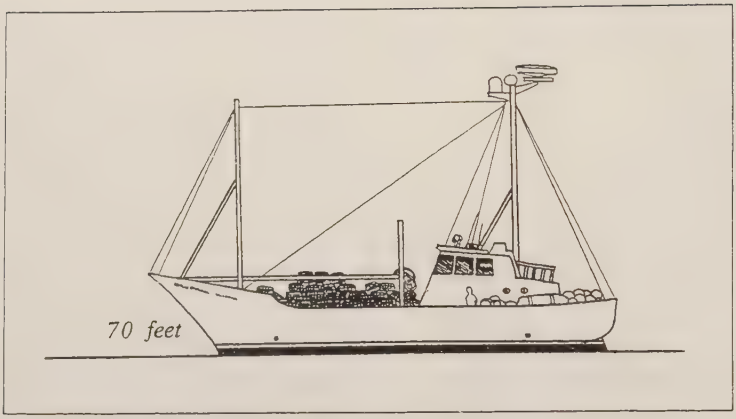

Figure 8.—Drawing of typical NWHI lobster boat.

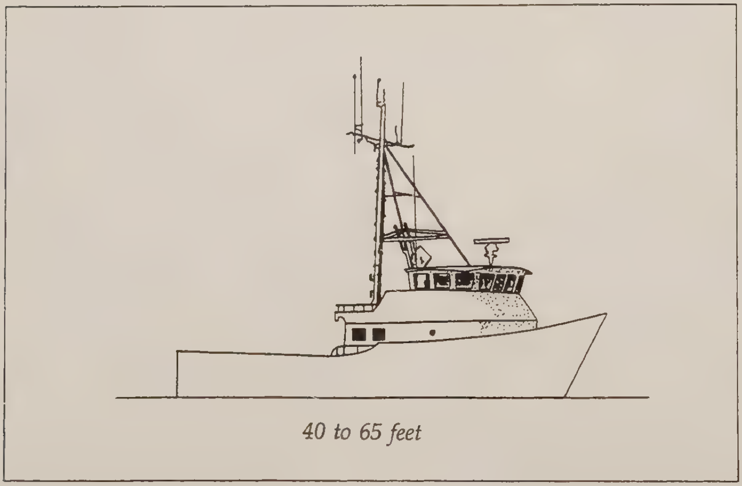

Figure 9.—Drawing of typical NWHI bottomfish boat.

velopment for the neighbor islands whose commercial fishery appeared to be left behind by the growth of the large-scale fishing fleets based in Honolulu. Today, there are strong local markets for fresh fish on the neighbor islands, associated with the expansion of the tourist trade on those islands, and there is considerable "export" of fresh fish to the U.S. mainland. However, access by handline boats to the higher value-added market has been limited on account of a phenomenon known as the "burnt tuna phenomenon," a condition in which the meat of handline and troll caught yellowfin tuna is metabolically degraded during fishing when not offset by rapid icing. Nonetheless, landings of tuna and other pelagics (primarily billfish, mahimahi, and ono) by troll, handline, and miscellaneous gears (i.e., excluding longline and aku boat) increased by elevenfold from 1970 to 1990 (Fig. 13).

In 1984 the tuna cannery Hawaiian Tuna Packers closed, coinciding with a period of substantial reorganization in the multinational canned tuna industry. As a result, the aku boat fleet declined from 12 active boats in 1979 (Hudgins, 1980) to just 7 active boats in 1986, selling solely to the fresh market (Boggs and Pooley, 1987; Pooley et al.[13]). Attempting to expand that market was a major project of State government in the 1980's (MacDonald et al., 1991), but current conditions in the fishery suggest that an entirely new start will be required, including a solution to the perceived bait problem and limitations on market penetration (primarily due to limited shelf life), if the potential yield of the skipjack resource is to be achieved in the future (Boggs and Pooley, 1987). Landings in the past five years have averaged less than 5 million pounds, with only 4 full-time aku boats active in the fishery.

By the mid-1980's, the export market for Hawaii's fresh bigeye tuna rose dramatically, largely as a result of marketing efforts by major wholesale dealers and the favorable exchange rate between the dollar and the yen. This marked the early resurgence of Hawaii's traditional longline tuna fleet, which produces a superior-grade tuna for sashimi (raw tuna). In the late 1980's, both NWHI bottomfish and lobster boats began facing lower catch rates and increased regulation, so that a number of these vessels began to transfer to the longline fishery.

In the early 1980's, perhaps as few as 15 vessels were fishing with longline gear in Hawaii. Today, over 150 vessels are in the longline fleet. Most of the vessels are newer and larger. Whereas the older sampans are about 45 feet, the new steel-hulled vessels range from 65 to 115 feet (Fig. 14). Many of the older vessels have new owners and have been refurbished. The longline crews have been trying a number of different fishing strategies, from fishing as far as 1,200 miles from Honolulu to fishing right off the reef,[14]

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[13] S. G. Pooley, S. Teramoto, and A. C. Todoki. 1988. Hawaii's aku fishery in 1986 and 1987. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent. Admin. Rep. H-88-16, 15 p.

[14] Fishing off the reef provides a major fisheries management controversy. The Western Pacific Fishery Management Council has closed the waters around the main Hawaiian Islands to

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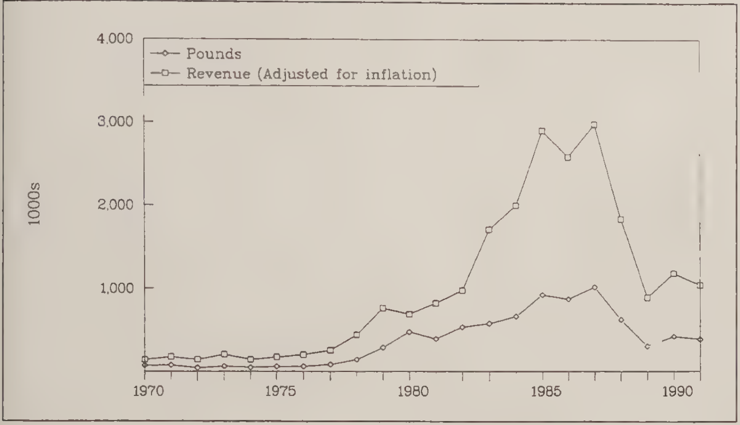

Figure 10.—NWHI bottomfish landings, pounds and revenue, 1970-91. NMFS estimates. Revenue adjusted for inflation to 1990 U.S. $ base.

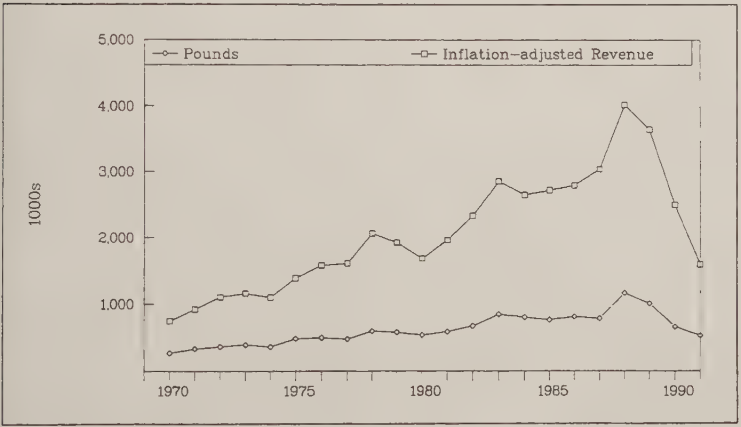

Figure 11.—MHI bottomfish landings, pounds and revenue, 1970-91. NMFS estimates. Revenue adjusted for inflation to 1990 U.S. $ base.

from fishing for the high-valued bigeye tuna to fishing for the lower-valued but more abundant yellowfin tuna, to long-distance fishing for swordfish destined for export to the east coast. The new vessels deployed a new gear which has now become the predominant gear throughout the Hawaiian longline fishery, the more efficient monofilament mainlines stored on reels, frequently set by powered line throwers (Kawamoto et al.[15]). The growth of the longline fishery is depicted in Figure 15.

Hawaii's market for fresh tuna (and other pelagics such as mahimahi) is now highly competitive, with competition in supply from Florida to Australia. The local fish market must now compete with the Tskuji market in Tokyo for the raw product, and local consumers must compete with the local restaurant trade and the export market.

If we take a brief look in retrospect, in 1979 the Hawaii Fisheries Development Plan predicted commercial fisheries growth to 50 million pounds in 1990 and 85 million pounds in the year 2000 (Department of Land and Natural Resources, 1979b). As one of the Plan's co-authors, I would say we failed to anticipate the likelihood and potential consequences of the collapse of U.S. production of canned tuna (the closure of the California and Hawaii canneries, and the emphasis on purse-seine tuna processing at the American Samoa and Puerto Rico canneries), and thus our forecasts for skipjack and albacore tuna landings were far afield. We also expected a rapid development of the oceanic shrimp fishery, but ultimately the resource did not support large-scale development (Tagami and Ralston[16]). But for ahi, NWHI lobster and bottomfish, the projections for growth have been quite reasonable. The prospects for further development in pelagics remain strong, although development must now be tempered by fisheries management considerations.[17]

## Fleets and Current Landings

Hawaii's commercial fishery exceeds $50 million in ex-vessel revenues, from 22 million pounds of landings in 1990. The longline tuna

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longline fishing and has imposed a moratorium on new entry into the Hawaii-based longline fishery from 1991 through 1994 (Amendments 2, 4, and 5 to the Fishery Management Plan for the Pelagic Fisheries of the Western Pacific Region, Western Pacific Regional Fishery Management Council, Honolulu, Hawaii 1986, as amended in 1991.)

[15] K. E. Kawamoto, R. Y. Ito, R. P. Clarke, and A. Chun. 1989. Status of the Hawaiian tuna longline fishery 1987-88. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-89-10, 33 p.

[16] D. T. Tagami and S. Ralston. 1988. An assessment of exploitable biomass and projection of maximum sustainable yield for *Heterocarpus laevigatus* (shrimp) in the Hawaiian Islands. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-88-14, 22 p.

[17] The relationship, or lack thereof, of fishery development and fishery management has been a difficult one. The Western Pacific Fishery Management Council initially tried to bridge the gap, but it had few resources which could be placed on fishery development issues. Within the State of Hawaii government, the two functions exist in different departments, while within NMFS, fishery development functions have been phased out since the late 1970's except for awards to private sector projects (the Saltonstall-Kennedy grants). Most State of Hawaii fishery

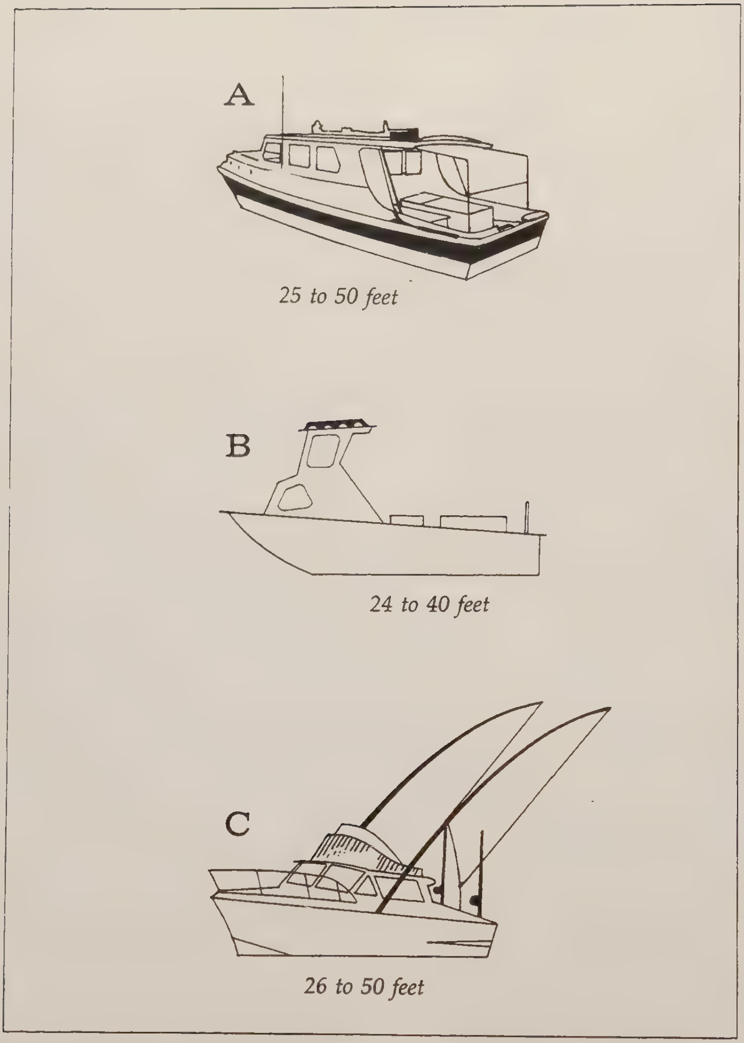

Figure 12.—Drawing of typical MHI (A) bottomfish, (B) pelagic handline, and (C) trolling boats.

fishery is the largest commercial fishery in Hawaii, valued at $29 million. The smaller-scale troll and handline fisheries for tuna and mixed pelagics, such as mahimahi, are next in value, at $7 million, while lobster, aku (skipjack tuna), and bottomfish (snappers, groupers, and jacks) are the other major commercial fisheries (Table 2).

While there were 15,000 boats registered (or documented) in Hawaii in the 1980's, only from 7,500 to 5,000 were used for fishing (Skillman and Louie[18], Sumida, et al.[19]; Meyer Resources Inc.[20]). Less than 2,000 vessels are presently registered for commercial fishing and, while there are less than 3,500 people holding commercial fishing licenses (issued to individuals), most commercial fishing license holders make minimal record of landings. There are perhaps only 750–500 boats that could be considered full-time commercial and charter-boat fishing operations. Almost all the fishing boats in Hawaii are less than 100 feet overall; only a portion of the longline fleet is longer than 75 feet.

This mixture of small and medium-sized fishing vessels has been relatively beneficial for Hawaii's fisheries (Pooley[21]). Large vessels can easily overharvest many of the nonpelagic resources while having a hard time making ends meet over the long run in such limited fisheries[22]. Many of the medium-sized vessels have the advanced technology and mobility to make switching between fisheries a viable business strategy[23], while at the same time not having a strongly negative impact on the small-scale commercial and recreational fishermen. Indeed, it was believed that Hawaii's offshore pelagic fisheries, which are substantially less susceptible to overfishing by small and medium-sized

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[17] *Continued*
conservation activities are oriented toward nearshore fisheries. The State's 1985 fishery development plan added an emphasis toward the noncommercial sectors Hawaii's fishery and warned: "Fisheries development can only be promoted for those fishery resources that can withstand increased fishing pressure without damaging the integrity of the resource. . . ." (Hawaii Division of Aquatic Resources, 1986).

[18] R. A. Skillman and D. K. H. Louie. 1984. Inventory of U.S. vessels in the central and western Pacific: Phase 2—verification and classification. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-84-12, 21 p.

[19] R. F. Sumida, B. M. Ito, and J. P. Draper. 1985. Inventory and uses of vessels in Hawaii, 1984. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., nontechnical report.

[20] Meyer Resources Inc. (P. A. Meyer.) 1987. A report on resident fishing in the Hawaiian islands. (A project to determine the economic value of recreational fishing in Hawaii.) U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-87-8C, 74 p.

[21] S. G. Pooley. 1985. The hopelessness of the invisible hand: small versus large fishing vessels in Hawaii. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-85-02, 16 p.

[22] For example, Clarke and Pooley (1988) found that mid-sized vessels (65 feet overall length) were the most profitable in the NWHI lobster fishery, while the larger vessels (greater than 75 feet in overall length) were not profitable. However, the larger lobster vessels have participated in the NWHI lobster fishery and have a dramatic impact on available stocks of lobsters.

[23] A strategy increasingly constrained by the implementation of limited entry in Hawaii's major commercial fisheries.

fishing vessels, would be an attractive avenue for future growth. Unfortunately the recent development of the longline fishery has been less benign, with substantial disputes amongst participants (Pooley, 1990).

The structure of Hawaii's seafood markets has encouraged value-added fisheries development (i.e., the production of a higher quality and higher-priced product through improved handling and marketing and the increased utilization of lower valued species), but with some definite side effects for Hawaii consumers (i.e., higher prices and lower availability). Whereas many mainland U.S. fisheries are "industrial-strength" with poor reputations for quality, low fresh fish prices, and poor incomes for fishermen, in Hawaii the combination of auctions and direct purchases from outside sources has meant a consistently high-quality product. However, fresh fish prices have risen considerably since 1970, even adjusted for the general rate of consumer price inflation (Fig. 16). This has been prompted by the explosion of restaurant demand, where fresh mahimahi can be found on local restaurant menus from Moiliili to Kaanapali, and on the U.S. mainland from Seattle to Des Moines to Boston. For local consumers, the loss of the aku (skipjack tuna) fleet has produced higher retail prices for fresh tuna. Our analysis of the price structure of Hawaii fresh fish prices (Pooley, 1987; Pooley[24, 25]) indicates that the market provides strong quality premiums and is thus a competitive forum for most major fishery producers. However, as the export market develops from the sashimi "niche" to the swordfish "segment," transshipping operations are increasing. This reduces the "local content" of Hawaii's fishery landings, at some detriment to Hawaii's economy and to local consumers.

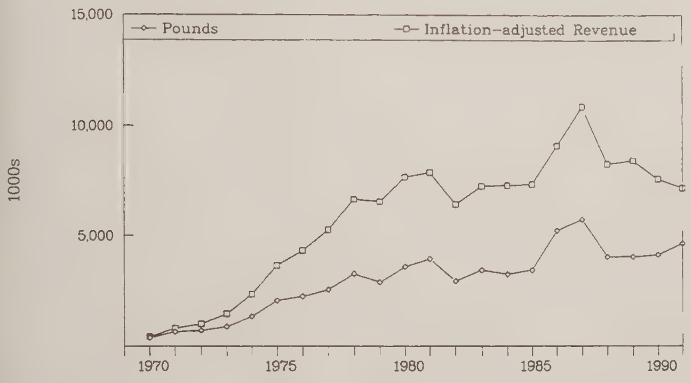

Figure 13.—MHI pelagic landings, pounds and revenue, 1970-91. NMFS estimates. Revenue adjusted for inflation to 1990 U.S. $ base.

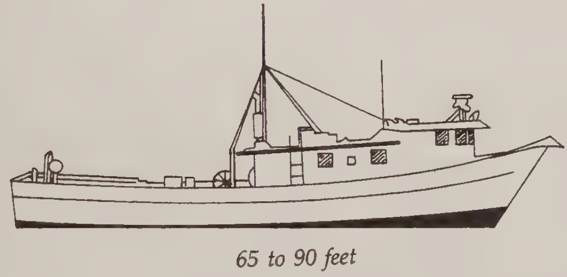

Figure 14.—Drawing of typical modern Hawaii longline boat.

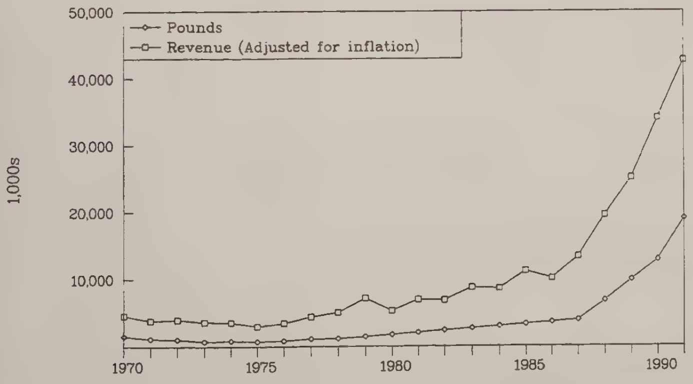

Figure 15.—Hawaii longline landings and revenue, 1970-91. NMFS estimates. Revenue adjusted for inflation to 1990 U.S. $ base.

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[24] S. G. Pooley. 1986. Competitive markets and bilateral exchange: the wholesale seafood market in Hawaii. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-86-08, 14 p.

[25] S. G. Pooley. 1991. Revised market analysis: Hawaii yellowfin tuna. NMFS Southwest Fish. Cent., Honolulu Lab. manuscr. 003-91H-MRF.

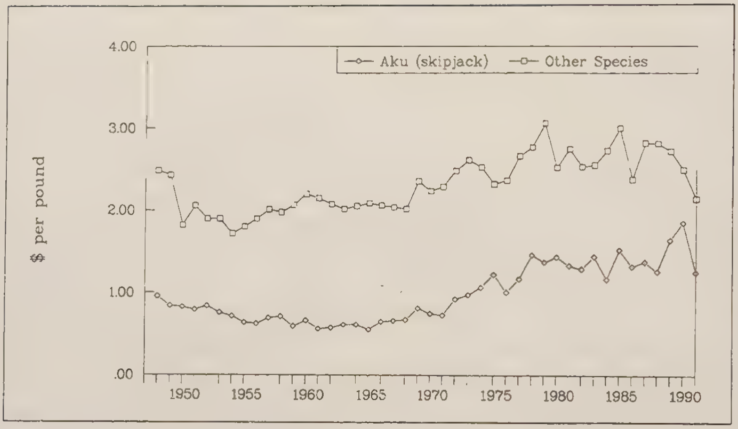

Figure 16.—Hawaii commercial fishery ex-vessel prices, 1948-91. U.S. $ per pound (whole weight). NMFS estimates, aku (skipjack tuna) and all other species. Prices adjusted for inflation to 1990 U.S. $ base.

### Recreational Fisheries

The distinction between "recreational" and "commercial" marine fishing in Hawaii's small boat fleets is extremely tenuous. As opposed to most mainland U.S. states, there is relatively easy access to most fishing locations by most residents of Hawaii. Furthermore, and perhaps most important, Hawaii's seafood market is not as centralized and industrialized as mainland fisheries, so that it has always been feasible for small-scale fishermen to sell any or all of their catch for a respectable price. Many people sell a portion of their catch to offset fishing costs, while division of the catch amongst family and friends is also a common practice and indeed in some circles, an important cultural and social obligation. Many people who might be considered "commercial" fishermen in fact hold a full-time or part-time job which provides more income than fishing. Furthermore, charter-fishing boat captains generally retain their catch for sale in the local market, unless explicit arrangements are made to the contrary.[26] Even the catch at major sports fishing tournaments is frequently sold by the charter captains. Not only are there overlapping structural factors in commercial and recreational fishing, but the legalistic differentiation is not particularly helpful. People who catch and sell at least a part of their catch are required to have a State of Hawaii commercial fishing license. However these licenses cost only $25 ($50 to nonresidents), and there is no marine recreational fishing license. Furthermore, there is no active dealer-reporting system, and Federal fisheries management has yet to require permits for the small-boat bottomfish and pelagic fleets.

Because of the lack of information on the small-boat fisheries, a number of survey approaches have been taken to estimate the extent of Hawaii's "recreational" fisheries. The most comprehensive was the NMFS Marine Recreational Fishing Statistical Survey (1979–81) which was a combined telephone and creel intercept survey.[27] The intercept included all modes of marine fishing: shoreline; piers and jetties, private vessel; and charter boat. The telephone and intercepts were fielded by a local company under contract to NMFS headquarters (with minimal actual involvement by NMFS staff in Hawaii), but the statistical expansions were undertaken by a firm on the mainland and delivered only to NMFS headquarters. For reasons not entirely understood, the expansions provided inconsistent estimates of various species and the results were never published. However, if we assume the major source of error was in individual species extrapolation, rather than in total participation and total or aggregate landings, then the following results can be derived.

The 1980 estimates of participation were 2.1 million fishing trips (620,000 by private boats and 88,000 by charter boats, the remainder being shoreside fishing) taken by 235,200 residents and 82,200 visitors (tourists). This amounted to 24% of the de facto resident population. The estimated weight of "recreational" fish caught was 4.4 million pounds, of which 94% was from boat fishing.[28]

In 1984, the Honolulu Laboratory, NMFS, and the Division of Aquatic Resources, State of Hawaii, conducted a survey of vessel owners registered with the State of Hawaii's Department of Transportation[29] (Skillman and Louie[30]; Sumida et al.[31]). Of the respondents who indicated they fished during the year, 70% said they never sold any of their catch, and only 16% sold at least half their catch.[32]

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[26] Reporting of catch by charter boats to the Hawaii Division of Aquatic Resources was formalized in 1985. Prior to that, some charter boats reported their catch, and others did not. Charter boats are not explicitly differentiated in the State commercial fish catch reports, although the commercial fishing license identifies these vessels.

[27] Data and methodology for the NMFS Marine Recreational Fishing Statistical Survey in the western Pacific were never published officially. These interpretations are based on project documents obtained by the Honolulu Laboratory several years after the survey was completed.

[28] These estimates were based on samples taken from the 8,033 people who were "intercepted" (sampled) in Hawaii. "Recreational" was not well defined, but is believed to indicate the fish weighed at the sample location were not to be sold. The expansion was based on 4,593 telephone interviews to Hawaii households, of which 15% contained people who went fishing.

[29] Of the approximately 14,500 vessels registered in 1984 with the State Department of Transportation (or documented with the Coast Guard in Hawaii), 12,578 were deemed to have fishing vessel characteristics (cruise liners were excluded, for example). Sixty percent of the questionnaires were completed, with 5,496 vessel owners reporting their vessel was used for fishing. No examination of the nonrespondents was made, so it is not known to what extent returns on this survey were self-selected from fishing vessel owners or not. Presumably 9,200 vessels (60% of the initial population of vessels) could have been used for fishing, but we have tended to use the lower figure as more realistic on the expectation that many people who did not use their boat for fishing would not bother to answer and return a survey oriented

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In 1987 the Hawaii Division of Aquatic Resources surveyed its license holders on a number of issues. Although the response rate was low (30% of the 2,529 license holders responded), the survey appears to confirm the impression that most "commercial" fishing license holders in Hawaii do not make their livelihood from fishing: 80% or more of the respondents on each island indicated they earned less than 51% of their gross income from fishing.

Karl Samples, University of Hawaii, prepared a series of studies on charter boat fishing during the early 1980's for NMFS. Samples found that the charter boat fleet consisted of 119 boats in 1982 (Samples et al.[33]). These vessels are almost entirely 2–6 passenger vessels where half-day and whole-day charters are sold to the group, rather than to individuals (as in U.S. mainland "head" and "party" boats). This fleet generated 73,780 passenger trips with a direct income of $8.1 million[34]. Total fish catch by the charter boat fleet was 2.2 million pounds. It was also estimated that charter boat patrons spent $39 million directly related to charter fishing as a vacation or leisure activity (Samples and Schug[35]).

The only major study of the economics of recreational fishing in Hawaii was undertaken by Meyer Resources Inc.[20] for NMFS. This study used a variation of the contingent (nonmarket) valuation technique on focus groups composed of recreational fishing clubs in Hawaii. Meyer estimated that there were 6,684 small boats used for "resident" fishing (defined as: "persons who are not making their primary living from commercial fishing," Meyer[20], p. 1) in Hawaii, with direct expenditures of $24 million. Total catch by these vessels was 21 million pounds, of which 47% was sold. The remainder was used for home consumption (23%), given away to friends and family (21%), or otherwise used. Using contingent valuation techniques, Meyer estimated that the nonmarket value of these fishing trips to Hawaii resident fishermen was $239 million.[36]

Finally, in 1990 and early 1991 the State of Hawaii, with the assistance of NMFS, conducted a survey of small boat launch sites and harbors on Oahu (the island on which Honolulu and 80% of the population is situated) to understand better offshore fishing by recreational and subsistence fishermen. The results from this survey may provide a stronger basis for estimating current recreational and part-time commercial fishing activity (Hamm and Lum[37]).

## Recent Issues

Naturally, the transition from the old style to the new in Hawaii's offshore fisheries has not occurred without biological, economic, and social impacts. Hawaii's commercial and recreational fisheries are no longer what they were, and the relationship between Hawaii's people and the sea has changed. We have already mentioned the change in availability and price of locally caught fish for Hawaii's resident consumers, but there have been changes in the water and on the docks too.

Recognition that nearshore fish resources have diminished (as well as consumer fears concerning ciguatera toxins), combined with the rise in tourism-related ocean recreation, means that there will be more pressure for nearshore marine environment management, with a premium on nonconsumptive uses of marine resources. A number of State of Hawaii initiatives have focused on this recognition, including the Main Hawaiian Islands - Marine Resources Investigation (Pooley[38] and Hawaii Division of Aquatic Resources, 1988), and there has been a broad strategic planning approach to coastal zone management and development (Hawaii Ocean and Marine Resources Council, 1991). Furthermore, rights of native Hawaiians to fishery resources are being explored, primarily through the offices of the Western Pacific Fishery Management Council (Iversen et al., 1989), and these will undoubtedly affect the ultimate resolution to fishery management issues. How Hawaii balances all of these interests may be a major political issue for the 1990's.

There are also some direct competitive pressures accompanying the rapid growth of the longline fishery. The Western Pacific Regional Fishery Management Council (Council) is the center of commercial fisheries management in Hawaii, whereas the state government is concentrating on nearshore fishing issues. The early years of the Council involved laying out a fishery management structure with relatively little emphasis on the distributive issues which were central on the

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[29] *Continued*
towards fishing. We also noted through inspection of the respondents that most of the full-time commercial fishing boats also did not respond.

[30] R. A. Skillman and D. K. H. Louie. 1984. Inventory of U.S. vessels in the central and western Pacific: Phase 2—verification and classification. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent. Admin. Rep. H-84-12, 21 p.

[31] R. F. Sumida, B. M. Ito, and J. D Draper. 1985. Inventory and uses of vessels in Hawaii, 1984. NMFS Southwest Fish. Cent., Honolulu Lab., nontechnical rep.

[32] Only 3% of the respondents said they made half their income from fishing, suggesting that the survey returns were biased toward small-scale recreational fishermen.

[33] K. C. Samples, J. N. Kusakabe, and J. T. Sproul. 1984. A description and economic appraisal of charter boat fishing in Hawaii. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-84-6C, 130 p.

[34] Income from charter fees was approximately $5.8 million while income from selling fish was $2.3 million.

[35] K. C. Samples and D. M. Schug. 1985. Charter fishing patrons in Hawaii: a study of their demographics, motivations, expenditures and

[35] *Continued*
fishing values. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-85-8C, 95 p.

[36] Nonmarket value means in this case what the participants thought their fishing "experience" was worth in market terms. Frequently this is termed "willingness to pay," as in "How much would you be willing to pay to continue fishing ....?" although that is not the precise approach used by Meyer.

[37] D. C. Hamm and H. K. Lum. 1992. Preliminary results of the Hawaii small-boat fisheries survey. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-92-08, 35 p.

[38] S. G. Pooley (Editor). 1988. Recommendations for a five-year scientific investigation on the marine resources and environment of the main Hawaiian islands. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Honolulu Lab., Southwest Fish. Cent. Admin. Rep. H-88-2, 22 p.

U.S. mainland. The NWHI lobster and bottomfish fishery management plans (FMP's) addressed limited fisheries with limited interaction with other fisheries. The pelagic species FMP's orientation was simply toward displacing foreign longline fishing in the Council areas. However, with the growth of the domestic longline fishery in the late 1980's, the Council was suddenly faced with competing domestic issues.

Resolving these pressures has involved a real trade-off between the cost of regulation, in terms of the cost of biological and economic research and in terms of changes in life-styles, and the potential benefits of well-managed natural resources. People who go fishing are frequently very independent, more so than most. All one needs to do is examine the vastness and isolation of their working environment. They are also our most accessible observers of oceanographic conditions and marine biology. It seems that more needs to be done to encourage their community of interests with the rest of Hawaii's ocean and coastal users.

Foreign and U.S. mainland fisheries and markets are also influencing Hawaii's marine fisheries either through biological resource pressure and environmental effects which have led to displaced fleets or changes in market conditions, or through more direct changes in seafood markets. Foreign longline and baitboat fisheries for tuna have fished the central Pacific for decades. Although foreign longline vessels are effectively precluded from fishing within 200 miles of Hawaii (including the NWHI), the tuna and billfish stocks they seek probably are sufficiently migratory to hypothesize an interaction between their distant-water capture and fishing conditions in Hawaii. Furthermore, a number of local entrepreneurs have been exploring the importation of fresh fish directly into Honolulu from foreign longline vessels fishing just outside the U.S. Exclusive Economic Zone. The U.S. purse seine tuna fleet has expanded dramatically into the South Pacific, and the U.S. albacore trollers are now fishing the South Pacific, both using American Samoa as a base. Guam and the Northern Mariana Islands are also used as transshipment centers for purse seine and longline fisheries. The apparent closing down of the Japanese, South Korean, and Taiwanese drift gillnet fleets fishing for squid and albacore tuna, due to their impact on sea birds and marine mammals, may affect both the commercial fisheries of the central Pacific and seafood markets. In addition, there are the potential impacts of ocean mining and other nonfishery related marine developments.

Ironically, perhaps one of the most important economic components of Hawaii's commercial fishing industry is not fishing at all; it is the resupply operations for the hundreds of foreign fishing boats and refrigerated transports which stop in Honolulu harbor for supplies. The direct economic impact of these vessels is $46 million annually (Hudgins and Iversen, 1990). The whole question of harbor infrastructure has been a thorny one even before the original fisheries development plan (Department of Land and Natural Resources, 1979b). Similarly, the relationship between fisheries development and fisheries management and between fisheries and other coastal zone activities (cf. Department of Land and Natural Resources, 1979a) are central to Hawaii's political agenda in the 1990's.

Commercial fishing and the expenditures of the recreational and subsistence fisheries do not comprise a large industry in Hawaii, not even as a percentage of the overall ocean sector, although they are larger than many sectors of diversified agriculture and manufacturing. But fishing has a number of important linkages to Hawaii's current industrial and commercial structure and to Hawaii's cultural heritage. The commercial, recreational, and subsistence fisheries of Hawaii are important barometers of conditions in the ocean environment. Those of us whose job it is to monitor the marine fisheries and to conduct applied research on those fisheries are constantly fascinated by the variation which is displayed. The purpose of this paper has been to provide a better historical framework with which policymakers and the public can assess Hawaii's marine fisheries.

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# Detection of contaminant and climate effects on spawning success of three pelagic fish stocks off southern California: Northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, and chub mackerel *Scomber japonicus**

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**Abstract.**–We describe a simple biostatistical model of reproductive success (logarithm of recruits/spawner) applied to three coastal pelagic fish stocks off southern California: northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, and chub mackerel *Scomber japonicus*. We used the model to detect possible influences of gross climatic conditions and contaminant loadings (particularly of metals and organochlorines) on reproduction in these three stocks. Data included several decades of annual estimates of recruitment and stock size, monthly measures of climate, and annual estimates of contaminant loadings; the model included a compensatory stock-size component before adding environmental effects. The study was meant to generate, rather than test, hypotheses. For the chub mackerel stock, we detected climate influences, but no contaminant influences, on reproductive success, which was usually high during conditions typical of El Niño–Southern Oscillation events. For the northern anchovy stock, we detected no climate or contaminant influences on spawning success; however, the negative results may reflect low statistical power, rather than absence of contaminant influences. For spawning success in the Pacific sardine stock, we detected no consistent climate influences, but we found a strong negative correlation with contaminant loadings. This result is consistent with the hypothesis that contaminant loadings accelerated the collapse of the Pacific sardine stock while it was under stress from severe overfishing. Although many scientific questions about validation of models, mechanisms of action, and identity of specific deleterious contaminants remain to be answered, the observed data are well described by the hypothesis of contaminant-mediated decline.

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In recent years, there has been increasing concern about possible effects of contaminants on the nation's living resources, particularly exploited fish and shellfish populations. Although contaminants such as heavy metals and synthetic organochlorines are commonly detectable in coastal sediments, waters, and organisms (Mearns et al. 1991), it has been difficult, if not impossible, to determine whether sublethal levels of contaminants have influenced the productivity of coastal fish stocks. Mass mortalities and deformities of fish and shellfish have occurred after exposure to high levels of contaminants, but mortality and morbidity in natural populations attributed to chronic low-level exposures is difficult to prove conclusively, even though it may be strongly supported by circumstantial evidence (Sindermann 1978).

In addition, the question of population-level effects has been largely unexplored. For individuals of most species, the physiological effects (if any) of chronic sublethal exposure to contaminants are poorly understood. For populations, the effects of such exposure are not known. Nonetheless, evidence from many studies of individuals suggests that populations should be affected also.

This paper describes exploratory models of the effects of contaminants, climate, and spawning-stock size on three exploited fish populations off southern California. With a rich body of data, this area is unusually well suited to such a study. The waters off southern California contain elevated levels of numerous contaminants, including PCBs, DDT, and several toxic metals (McCain et al. 1988). Estimates of historical contaminant loadings have been made by Summers et al. (1988), and data on climatic conditions are available from public records. Major coastal pelagic fisheries have been monitored by the California Department of Fish and Game since about 1930.

Two main conceptual approaches might be used to model the effects of contaminant exposure on populations. The first approach is a "bottom-up" one: constructing a mechanistic population model that somehow extrapolates known effects on individual organisms to effects at the population level. The second approach is entirely at the population level: construction of statistical models that correlate historical changes in population properties (especially properties thought to be sensitive to environmental fluctuation) to changes in contaminant loadings.

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Neither of these approaches is completely satisfactory. Weighing against the first approach is the fact that the existing theory of population biology does not allow extrapolation from physiology and behavior of individuals to the net productivity of the population. Indeed, biological populations seem to have emergent properties unknowable from the observable properties of individuals (Mayr 1982). A similar problem is that combinations of contaminants may work in unforeseen ways; one might say that such combinations have their own emergent properties. Thus the biological activity and availability of mixtures of contaminants in the coastal environment are difficult, if not impossible, to extrapolate from laboratory studies of exposure to individual contaminants. Given the seemingly insurmountable barriers to constructing mechanistic bottom-up models of populations chronically exposed to low levels of contaminants, we used the alternative approach: we constructed empirical statistical models of contaminant effects on populations. The empirical approach, of course, also has many limitations; these are discussed at length in later sections.

## Model structure

Evidence suggests that the youngest stages of fishes should be most sensitive to the effects of contaminants (Weis & Weis 1989). For that reason, our model of contaminant effects addresses survival from the egg stage to age of recruitment (roughly the first year of life). The model is based on the widely-used Ricker (1954) model of fish recruitment:

$$R = \alpha P e^{-\beta P} \zeta, \tag{1}$$

where $R$ = recruitment in number of fish or biomass,
$P$ = parent spawning-stock size (usually spawning biomass),
$\alpha, \beta$ = estimated parameters of the Ricker model,
$e$ = base of natural logarithms, and
$\zeta$ = a lognormally-distributed stochastic component with zero mean.

A common interpretation of Eq. 1 is that $\alpha$ represents the net fecundity of a unit of spawning biomass and $\beta$ reflects the degree of density-dependence in the stock's recruitment.

The Ricker model is often expressed in terms of the natural logarithm of recruits per spawner:

$$\log(R/P) = a + bP + \varepsilon, \tag{2}$$

where $a = \log(\alpha)$, $b = -\beta$, and $\varepsilon = \log(\zeta)$. (The sign change in $b$ is made merely to simplify the notation; $b$ is negative in a compensatory stock.) Assuming that the total number of eggs spawned is proportional to the spawning biomass $P$, the quantity $R/P$ is an index of an egg's probability of survival to recruitment. This seems to be a more appropriate quantity to use for detecting exogenous effects than recruitment itself, which is usually held to depend in the first order upon stock size. We refer to the quantity $R/P$ as "spawning success" and to its natural logarithm as "log spawning success." The model of log spawning success (Eq. 2) is linear in the parameters and contains an additive error structure, and thus can be fit by ordinary least-squares (OLS) regression.

Eq. 2 can easily be modified to incorporate external variables, such as climate or contaminant effects, that might affect spawning success. Suppose we have $m$ such variables, $\{x_1, x_2, ..., x_m\}$, for which we wish to estimate parameters $\{\theta_1, \theta_2, ..., \theta_m\}$. Then a model including these variables is

$$\log(R/P) = a + bP + \sum_{i=1}^{m} \theta_i x_i + \varepsilon. \tag{3}$$

In this expanded model, $m$ explanatory variables and population size affect log spawning success in an additive manner. The application of this linearized model is described in a later section. Other adaptations of the Ricker model to represent contaminant effects were made by Goodyear (1983) and Vaughan et al. (1984).

## Data sources and processing

Two main categories of data were used in this study: data on fish abundances, and explanatory data on the environment. Data on fish populations comprised time-series of age-structured abundance estimates from virtual population analyses (VPA). We examined three coastal pelagic stocks off southern California: northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, and chub mackerel *Scomber japonicus* (known locally as Pacific mackerel).

These stocks were chosen because they have each supported major fisheries and have been studied sufficiently well so that long time-series of stock and recruitment data are available. These coastal pelagic species also form a conspicuous part of the California Current ecosystem.

Explanatory data (data on the environment) included time-series of two types: variables related to climate, and variables reflecting contaminant loadings or other potential human impacts. These data were subjected to a number of stages of preliminary processing, including two principal component analyses, to compute two sets of derived variables (principal components) from a larger number of potential explanatory variables.

### Data on fish abundances

Stock and recruitment data on northern anchovy (Table 1, Fig. 1) were obtained from Table 8 of Methot (1989), who derived his estimates from fishery statistics and research survey data. For spawning-stock size, we used

**Table 1**

Stock and recruitment data used for modeling effects of contaminants and climate on spawning success of three pelagic fish stocks off southern California. Data on chub mackerel have traditionally been reported, maintained, and analyzed in the English system, and are so reported here.

| | Northern anchovy *Engraulis mordax* | | Pacific sardine *Sardinax sagax* | | Chub mackerel *Scomber japonicus* | |
|---|---|---|---|---|---|---|
| Year | Spawning biomass $10^6$t | Recruitment $10^9$ fish | Spawning biomass $10^3$t | Recruitment $10^6$ fish | Spawning biomass $10^6$ lbs | Recruitment $10^6$ lbs |
| 1946 | — | — | 566 | 3875 | 97.87 | 20.11 |
| 1947 | — | — | 405 | 4261 | 57.91 | 139.20 |
| 1948 | — | — | 740 | 3690 | 28.90 | 70.92 |
| 1949 | — | — | 793 | 290 | 72.43 | 11.21 |
| 1950 | — | — | 780 | 397 | 89.46 | 3.59 |
| 1951 | — | — | 277 | 972 | 72.05 | 3.80 |
| 1952 | — | — | 136 | 1197 | 32.89 | 55.35 |
| 1953 | — | — | 202 | 382 | 10.62 | 106.48 |
| 1954 | — | — | 239 | 264 | 38.58 | 45.90 |
| 1955 | — | — | 170 | 588 | 80.69 | 91.41 |
| 1956 | — | — | 108 | 1586 | 95.00 | 20.05 |
| 1957 | — | — | 90 | 905 | 77.30 | 28.00 |
| 1958 | — | — | 177 | 288 | 36.98 | 91.81 |
| 1959 | — | — | 122 | 111 | 33.59 | 70.18 |
| 1960 | — | — | 88 | 74 | 63.02 | 128.67 |
| 1961 | — | — | 54 | 56 | 81.32 | 85.60 |
| 1962 | — | — | 27 | 11 | 133.10 | 18.18 |
| 1963 | — | — | — | — | 168.65 | 9.58 |
| 1964 | 639,210 | 38.6 | — | — | 112.05 | 2.67 |
| 1965 | 531,520 | 13.4 | — | — | 44.27 | 4.21 |
| 1966 | 541,880 | 13.3 | — | — | 17.63 | 5.75 |
| 1967 | 409,170 | 27.9 | — | — | 4.11 | 1.14 |
| 1968 | 396,260 | 19.8 | — | — | 2.57 | 4.08 |
| 1969 | 374,300 | 33.1 | — | — | — | — |
| 1970 | 321,880 | 73.1 | — | — | — | — |
| 1971 | 333,600 | 123.3 | — | — | — | — |
| 1972 | 588,460 | 154.2 | — | — | — | — |
| 1973 | 1,812,900 | 114.9 | — | — | — | — |
| 1974 | 1,481,160 | 32.6 | — | — | — | 10.15 |
| 1975 | 1,458,430 | 14.3 | — | — | 0.63 | 2.53 |
| 1976 | 1,050,180 | 57.2 | — | — | 5.00 | 138.43 |
| 1977 | 868,890 | 6.5 | — | — | 22.68 | 89.87 |
| 1978 | 435,370 | 114.3 | — | — | 95.06 | 252.20 |
| 1979 | 582,890 | 82.0 | — | — | 166.36 | 35.40 |
| 1980 | 798,280 | 74.0 | — | — | 255.27 | 185.41 |
| 1981 | 782,770 | 19.7 | — | — | 332.28 | 158.58 |

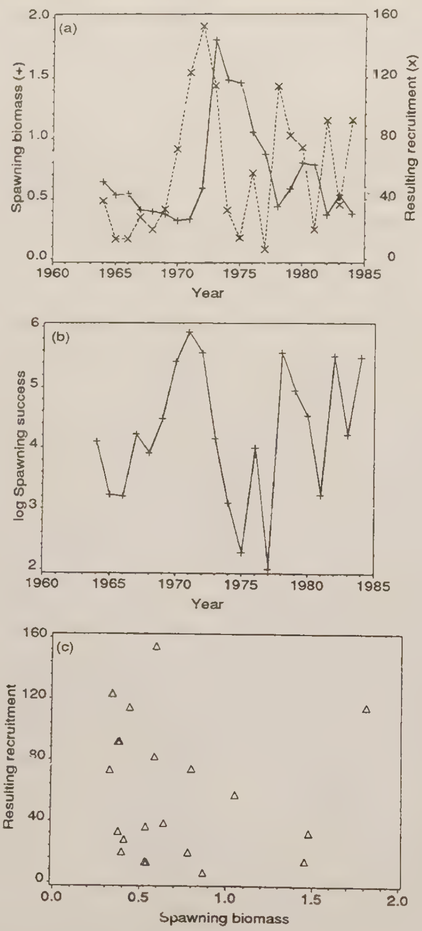


**Figure 1**

Recruitment of the northern anchovy *Engraulis mordax* stock off southern California. **(a)** Time trajectories of recruitment $R$ ($10^9$ fish) and spawning biomass $P$ ($10^6$t); **(b)** time trajectory of log ($R/P$); **(c)** stock-recruitment scatterplot, in same units as (a).

Methot's estimates of spawning biomass on 15 February of each year. For recruitment, we used Methot's estimates of the number of recruits on 1 July of the same year. Methot stated that his estimates of recruitments before 1964 are much less precise; we used his estimates of 1964 through 81 (the end of the contaminant data series).

Stock and recruitment data on Pacific sardine (Table 1, Fig. 2) are the estimates of MacCall (1979, Table 3), and were derived from fishery statistics. Although the estimates extend through 1964, MacCall (1979) discounted the 1963 and 1964 estimates of recruitment as not sufficiently precise. We used the estimates from 1946 (the beginning of the contaminant series) through 1962.

Stock and recruitment data on chub mackerel (Table 1, Fig. 3) are from Table 1 of Prager & Hoenig (1989), who compiled data from MacCall et al. (1985), Parrish & MacCall (1978), and Prager & MacCall (1988a). The estimates, all derived from fishery statistics, were adjusted by Prager & Hoenig (1989) to a common reporting date. The temporal limits of our analysis, 1946–81, were determined by the limits of the contaminant series. The chub mackerel data span a stock collapse and subsequent closure of the fishery and thus have 6 yr (1969–74) of data missing. Nonetheless, the chub mackerel series ($n$=30) is the longest of the three stocks. The data encompass at least two distinct epochs in the existence of the population: the pre-collapse epoch of steadily increasing exploitation rate, and the post-collapse epoch of more strictly regulated fishing and the associated population increase.

## Explanatory data: Contaminants

Historical contaminant-loadings data were compiled and reconstructed by Summers et al. (1988) according to a mass-balance approach based on manufacturing volume, land use practices, and mobility of particular contaminants. Summers et al. (1988) also compiled more general measures (e.g., wastewater flow) from governmental records. The resulting annual time-series include five major categories: gross indicators, physical-biological factors, nutrient loadings, organochlorine loadings, and metal loadings (Table 2). Prager & MacCall (1990) discussed the loading patterns of individual contaminants and provided time-series plots of each; here, we review major characteristics abstracted from Summers et al. (1988) and Prager & MacCall (1990).

The human population of southern California has increased sharply over the last 50 yr, and this is reflected in many contaminant-loading patterns, particularly in the first three categories (Table 2). For example, loadings of nitrogen, phosphorus, and total organic carbon arise principally from wastewater (sewage) flow, which has increased with population size; power-plant cooling flows, for the most part, also reflect the growing population's use of electricity. While size of the annual kelp harvest is strongly correlated with human population size, the relationship may be noncausal; this is impossible to ascertain statistically. Nonetheless, size of the kelp harvest was included among other potential indicators of environmental stress, as many species are present in kelp-forest habitat during early stages of life history.

With the exception of PCBs, the organochlorines listed in Table 2 were all introduced in the late 1940s. Most fluctuations in individual loadings have followed legal restrictions on use (e.g., of DDT) and subsequent increased use of

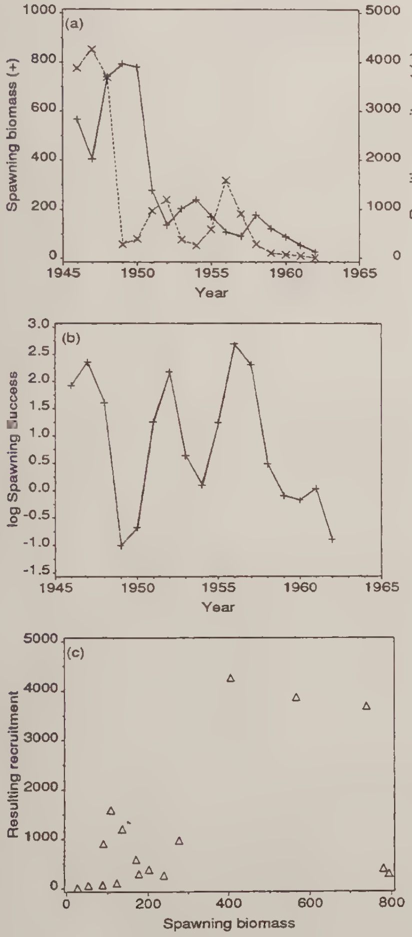


**Figure 2**

Recruitment of the Pacific sardine *Sardinops sagax* stock off southern California. **(a)** Time trajectories of recruitment $R$ ($10^6$ fish) and spawning biomass $P$ ($10^3$t); **(b)** time trajectory of log ($R/P$); **(c)** stock-recruitment scatterplot, in same units as (a).

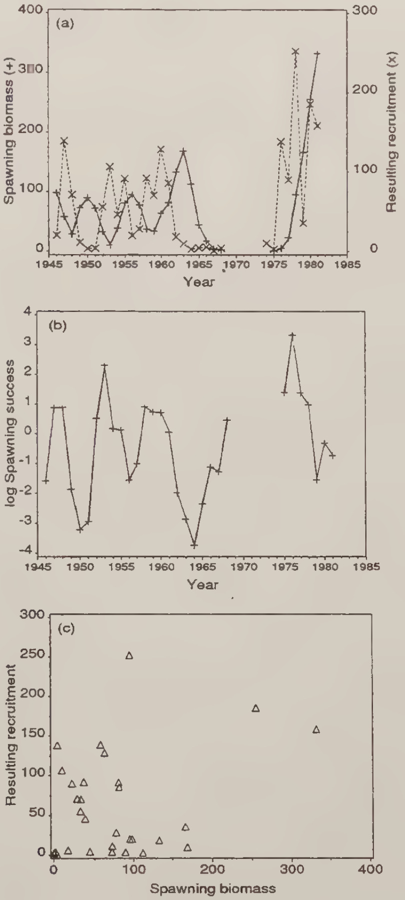


**Figure 3**

Recruitment of the chub mackerel *Scomber japonicus* stock off southern California. **(a)** Time trajectories of recruitment $R$ ($10^9$ lb) and spawning biomass $P$ ($10^9$ lb); **(b)** time trajectory of log ($R/P$); **(c)** stock-recruitment scatterplot, in same units as (a).

other pesticides. The sharp rise in pesticide use in the 1950s and the subsequent decline in the 1960s and 1970s are similar for many of these compounds, which leads to difficulty in distinguishing their effects statistically. The PCBs, a group of non-pesticide toxic organochlorine compounds, have been used increasingly throughout most of this century, but little is known about the volume of their use and discharge before 1960.

Loadings of metals have varied with growth of the human population and also with fluctuations in patterns of industrial use. Loadings of some particularly toxic metals, such as lead and cadmium, have declined recently because of environmental regulations.

Most of the historical reconstructions of Summers et al. (1988) included values for all years from 1946 through 1981, but some contaminant variables lacked values for 1981. We extrapolated from immediately-

### Table 2

Data available on contaminant loadings and other human impacts to the coastal waters of southern California, used for modeling spawning success of three coastal pelagic fish species. Headings indicate major categories. Variables were also assigned to groups (in parentheses) for principal-components analyses, used to reduce the number of variables before modeling. Asterisks (*) indicate variable not used for modeling.

| Type of data | Years available |
|---|---|
| **Gross indicators (Indicators group)** | |
| Human population | 1890–1980[a] |
| Municipal wastewater flow* | 1890–1985 |
| **Physical-biological factors (Indicators group)** | |
| Kelp harvest | 1916–1985 |
| Dredging volume | 1900–1983 |
| Power-plant cooling flow | 1928–1985 |
| **Nutrient loadings (Indicators group)** | |
| Nitrogen | 1910–1986 |
| Phosphorus | 1910–1986 |
| Total organic carbon | 1910–1986 |
| **Organochlorine loadings (Organochlorines group)** | |
| Aldrin | 1945–1982 |
| BHC or Lindane | 1945–1982 |
| Chlordane | 1945–1982 |
| DDT | 1945–1982 |
| Dieldrin | 1945–1982 |
| Endrin | 1945–1982 |
| Heptachlor | 1945–1982 |
| Polychlorinated biphenyls | 1929–1986 |
| Toxaphene | 1945–1982 |
| **Metal loadings (Metals group)** | |
| Cadmium | 1920–1980[b] |
| Chromium | 1929–1980[a] |
| Copper | 1929–1980[b] |
| Mercury | 1929–1980[a] |
| Nickel* | 1945–1980[c] |
| Lead | 1929–1980[b] |
| Zinc | 1929–1980[b] |

[a] Value for 1981 extrapolated from 1979 and 1980 values.
[b] Value for 1981 set equal to 1980 value.
[c] Time-series contains missing values within this period.

preceding values as necessary (Table 2). The extrapolated 1981 values, although necessary for the principal-component analyses, had very little influence on later calculations.

The reconstructions of Summers et al. (1988) comprise the best available dataset, and the only one on this scale, describing contaminant loadings off southern California in recent decades. Because of this, verification is difficult. Prager & MacCall (1990) found that the reconstructions agreed fairly well with some recent estimates of metals loadings made by the Southern California Coastal Water Resources Project (SCCWRP), which has monitored fluxes of metals from southern California sewage outfalls since 1971 (Konrad 1989). However, only a small portion of total metals loadings are in sewage; this may have caused the discrepancies noted for some metals by Prager & MacCall (1990). We also compared reconstructions with a study of metals deposition in anaerobic sediments in the Santa Barbara basin (H. Schmidt & C. Reimers, Scripps Inst. Oceanogr., La Jolla CA, pers. commun.). However, the sedimentary record, much less precise than the reconstructions, was unable to discern any clear trends or patterns in metals since 1932.

## Explanatory data: Climate

A large suite of climate data (Table 3) for the years 1920–84 was compiled by Prager & MacCall (1987a,b,c), who described the data sources and processing in detail. Most of the raw data were provided by Dr. Andrew Bakun (Pac. Fish. Environ. Group, NMFS Southwest Fish. Sci. Cent., Monterey CA).

We detrended most of the sea level (SL) and sea-surface temperature (SST) series to remove rising trends with time. Values for 1983 were not used in computing trend lines, to prevent this extreme El Niño year near the end of the series from distorting the results. Only the series of SST in San Diego did not exhibit a significant trend, and accordingly that series was not detrended.

Seasonal effects were removed by standardizing each variable to zero mean and unit standard deviation (SD) by month of year. For example, the January values (1920–84) of Los Angeles rainfall were standardized as a group to mean 0.0 and SD 1.0. Standardization was performed separately for each month and time-series.

The climate dataset had a few missing values that we replaced with estimates. We used the BMDP procedure AM (Dixon et al. 1983) to estimate these values by stepwise regression on the available data. Reasonableness of the estimates was verified by simulation and by comparison with the nonmissing data (Prager & MacCall 1990).

## Principal-component analyses

Many of the explanatory variables contained redundant information. For example, sea-surface temperature and sea level exhibit very similar patterns over time, as both are related to El Niño conditions and the flow of the California Current. Another example, noted above, is that many contaminant time-series are tightly

### Table 3

Summary of climate data used for modeling spawning success of three coastal pelagic fish stocks off southern California. Headings indicate major categories. Variables were also assigned to groups (in parentheses) for principal-component analyses used to reduce the number of variables before modeling.

| Type of data and station location(s) | Years of monthly data available |
|---|---|
| **Rainfall (Rainfall group)** | 1920–1984 |
| San Francisco, Oakland | |
| Los Angeles, Long Beach | |
| San Diego | |
| **Seawater salinity (Rainfall group)** | 1920–1984 |
| Scripps Pier: surface | |
| Scripps Pier: bottom | |
| **Sea-surface temperature (El Niño group)** | 1920–1984 |
| Farralon Islands | |
| Pacific Grove | |
| San Luis Wharf | |
| San Diego | |
| **Sea level (El Niño group)** | 1920–1984 |
| San Francisco | |
| Los Angeles | |
| San Diego | |
| **Bakun's upwelling index (Upwelling group)** | 1946–1984 |
| 30°N, 119°W | |
| 33°N, 119°W | |
| 36°N, 122°W | |
| 39°N, 122°W | |

coupled to human population size, which generates them. This multicollinearity causes problems in fitting and interpreting statistical models such as ours. In extreme cases of multicollinearity, numerical algorithms used for fitting can fail. A more likely problem is that interpretation is not straightforward, because parameter values depend upon the other variables in the model. When sea-surface temperature is included in a model, for example, it may explain a large amount of the variance associated with sea level, so there is little to be gained from including sea level itself in the model. Yet an effect may truly be due to sea level (or to the strength of the California Current), and this relationship may thus be overlooked. Because of this difficulty, any biostatistical study of this nature is inherently unable to isolate the effects of individual causes. An important related practical problem is that a large number of potential explanatory variables makes any fitting procedure unwieldy.

We addressed some of these statistical problems by combining the explanatory data into new composite variables that did not contain duplicate information. These new variables, constructed by principal-component analysis, are linear combinations of the original variables. To reduce the number of variables (initially ~216) to a number more easily analyzed by standard statistical software, data on sea level, sea-surface temperature, and salinity were converted to bimonthly means; also, surface and bottom salinities at Scripps Pier were averaged. Monthly rainfall values were transformed into an annual value of total rainfall (preceding 1 July to current 30 June) and a value representing the median date of the season's rainfall. The explanatory dataset with these changes contained 94 variables before reduction by principal-component analysis.

We constructed two separate sets of principal components. The first set was constructed from physical and climate data (Table 3) but not data on contaminants or general stressors (Table 2). A recruitment model based on this analysis would show how much of the variability in spawning success could be attributed to stock size and climatic variation alone. The second principal-component analysis included all explanatory variables, and was used to reveal how much more variability could be explained by adding contaminant information to the analysis.

Weighting was used in the principal-component analyses to avoid giving undue emphasis to variables (e.g., SST) measured at many locations. To determine weights, each variable was assigned to one of six groups, as shown in Tables 2 and 3. Each group received 1/6 of the total weighting, which was divided equally among the variables within the group.

The results of principal-component analyses are frequently difficult to interpret, as the components are formed on purely statistical grounds. Extensive graphical analysis (presented in Prager & MacCall 1987c, 1990) allowed attaching an interpretation to some, but not all, of the components used in these analyses (Table 4). In interpreting results of the recruitment models, we used a different approach, that of measuring the correlation of the model's explanatory effect with the individual variables, as explained below.

## Application of model to three fish stocks

### Overview

For each stock, we developed two alternative models: one using the principal components of climate data only, and the second using the principal components of climate and contaminant data. We then examined correlations of each model's estimated explanatory time-series (i.e., the summation on the right side of Eq. 3) to the original climate and contaminant variables. Be-

**Table 4**

Interpretation of principal components (PCs) used as explanatory variables in models of spawning success in three coastal pelagic fish stocks off southern California. Variables $W_1$–$W_{10}$ are PCs of data on climate; variables $C_1$–$C_{10}$ are PCs of data on climate and on contaminant (e.g., metals, organochlorines) loadings. Because interpretation of PCs is difficult, other methods were used to interpret model results (Fig. 4–6; text). SST = sea-surface temperature, SL = sea level.

| Variable | Interpretation |
|---|---|
| $W_1$ | Heavy rainfall; elevated SL and SST; $W_1$ has peaks in 1958 and 1983 corresponding to El Niño events. |
| $W_2$ | Very low rainfall, high SST and SL in second half of year. |
| $W_3$ | Increased upwelling, especially in mid-year. |
| $W_4$ | Late rainy season with lower-than-average rainfall, decreased SST at northern stations. |
| $W_5$ | Reduced upwelling at 30°N station, late rainy season. |
| $W_6$ | Late rainy season in San Francisco. |
| $W_7$ | Heavy rainfall in San Francisco, high early-year salinity in La Jolla. |
| $W_8$ | No clear interpretation. |
| $W_9$ | No clear interpretation. |
| $W_{10}$ | No clear interpretation. |
| $C_1$ | Increased upwelling midyear; high loadings of metals, nutrients, and most organochlorines; $C_1$ is in part a trend component, increasing from 1945 to 1978 and declining slightly thereafter; |
| $C_2$ | High loadings of organochlorines, Cd, Cr, and Pb; reduced rainfall. |
| $C_3$ | Elevated SL and SST, heavy rainfall; highest in years of El Niño events. |
| $C_4$ | Elevated upwelling, especially at 30°N station; high loadings of Cr and BHC; $C_4$ is high around 1970, lower in other years. |
| $C_5$ | Early, wet, rainy season, especially in San Francisco. |
| $C_6$ | High loadings of Hg, early rainy season in southern California. |
| $C_7$ | No clear interpretation. |
| $C_8$ | No clear interpretation. |
| $C_9$ | No clear interpretation. |
| $C_{10}$ | No clear interpretation. |

cause one of the models contained no contaminant data, agreement between the two models on the importance of contaminant variates was considered an indication of severe and troublesome collinearity between relevant climate and contaminant variables. Alternatively, it might simply indicate no contaminant effects. In the presence of strong contaminant effects, and lacking such severe collinearity, one would expect the explanatory effect from the model including contaminants to be more highly correlated with the contaminant variables.

## Selection of explanatory variables

It is widely recognized by modelers and statisticians (e.g., Gilchrist 1984:11) that a profound source of uncertainty in statistical modeling is the possibility of error in specifying the model's structure. Such specification error biases parameter estimates and renders most confidence intervals and hypothesis tests invalid (Kennedy 1979, Gilchrist 1984). Unfortunately, the possibilities of specification error and its ramifications are often overlooked when statistical models are used in ecology. The models chosen and presented here were undoubtedly misspecified; they may have included unimportant effects or omitted important ones, and they were limited to a linear functional relationship, which is unlikely to be the true one.

After specifying the linear structure of Eq. 3, choice of variables was the main concern. When no theoretical basis exists to guide it, choice of variables in a regression model must be regarded as heuristic. Neither the theory of the underlying discipline—ecology—nor that of statistics can answer this question unequivocally, so we were forced to use an empirical approach. We started by retaining only the first 10 components from each of the principal-component analyses. (In each case, this retained ~80% of the weighted variance.) To arrive at a parsimonious model, we fit regression models to all combinations of 10 or fewer variables and ranked the many models by $C_p$, a goodness-of-fit statistic from Mallows (1973). For each combination of stock and data type (climate or combined), we accepted the model with the lowest $C_p$. However, alternative models of similar fit were similar in structure.

Any method of variable selection in which many candidate explanatory variables and combinations of variables are examined may lead the investigator to accept models which fit well solely through chance. This point has recently been emphasized by Flack & Chang (1987). Although the use of $C_p$ is a relatively conservative approach, the true statistical significance of our results is unknown. Thus we view the modeling exercise as one of hypothesis generation, rather than hypothesis testing. The limitations of inference that come from an empirical choice of model structure are not unique to this study; they pertain to all modeling exercises except those in which the final model structure and set of explanatory variables are correctly chosen before fitting. Here, we use elements of hypothesis testing, but acknowledge the impossibility of testing the hypotheses rigorously.

### Detecting the influence of contaminants

We started with the following null hypothesis: "any apparent influence of contaminants can be explained by random variability alone, including chance correlations of contaminant loadings with climate variability." We imposed three statistical criteria to be met before we would consider rejecting this null hypothesis on the basis of a model including contaminant-loadings data. The first criterion was qualitative: the correlations of the model's explanatory effect with most contaminant variables had to be negative. The other criteria were quantitative: the regression coefficients of the model had to be statistically significant at $\alpha$=0.05, and the inclusion of contaminant information had to provide more explanatory power than use of climate data alone. If all three criteria were met, we would admit the possibility of contaminant influence on spawning success. The three criteria are described in more detail immediately below.

**Sign test** Of the variables in Table 3, the metals and organochlorines have been found by bioassay to have deleterious effects on fish (Weis & Weis 1989). (We omitted nickel because of an incomplete time-series and, more importantly, its relatively low toxicity.) Power-plant cooling flow also is generally considered deleterious, but the remaining variables in the indicators group could be favorable as well as unfavorable. The signs of the correlations with the 16 "deleterious" variables were subjected to a (one-tailed) statistical test of the following null hypothesis: "The observed number of negative correlations could arise by chance alone." Under this null hypothesis, the probability of a negative correlation between a contaminant variable and the model's estimated explanatory time-series is 0.5. Assuming independence among the 16 contaminant variables (an assumption that may be violated; see below), the probability of obtaining $x$ negative correlations by chance is given by the binomial probability f(x; $n$=16, $p$=0.5). The probability of observing 11 or more negative correlations is 0.105, and of observing ≥12 is 0.038. Thus, the conventional error rate of $\alpha \leq 0.05$ requires ≥12 negative correlations between the 16 deleterious contaminant variables and the explanatory time-series from a model that uses the combined explanatory data.

Such a test concludes that apparent contaminant effects are qualitatively significant if 12 or more negative correlations are found. However, the true probability of Type-I error is >0.038, because many of the contaminant variables are positively correlated with one another, violating the assumption of independence in the binomial probability model and increasing the tail probabilities. While we cannot calculate an exact critical value of $x$ in view of lack of independence, the value would be larger than the nominal value of 12 required for a model to pass this test.

**Test of coefficients** This test was used to assess whether the coefficients of the chosen model were significantly different from zero. Although we always chose the model with lowest $C_p$, that criterion does not depend directly on how precisely the regression coefficients are estimated. To test the significance of regression coefficients, we used the standard $t$-tests (at $\alpha$=0.05) provided by the statistical software, and required all coefficients to be significant for the model to pass the test.

**Improvement-in-fit test** Our third criterion required that the model that incorporated contaminant information (i.e., which used the combined explanatory data) had to provide a substantially better fit to the spawning success data than the model using the climate data alone. To judge this, we used the Schwarz criterion (Smith 1988), a statistic for comparing non-nested models. The Schwarz criterion requires an estimate of $\sigma$, the true model variance; we used the MSE of the better-fitting model. To pass the test, the model with combined data was required to have a higher value of this statistic than the model with climate data.

## Results

### Northern anchovy

Not unexpectedly for a short-lived species, the spawning biomass of this northern anchovy stock appears to depend strongly upon the preceding few years' recruitments. A peak in spawning biomass generally follows a corresponding peak in recruitment by 1 or 2yr (Fig. 1a). The stock-recruitment relationship, although noisy, appears density-dependent, in that spawning success improves at lower stock sizes (Fig. 1c), and each model includes a significant compensatory term (the negative stock-size parameter; Table 5). Ricker (1954) and MacCall (1980) have pointed out that cannibalism of eggs or larvae by the adults could cause such compensation.

Neither the climate model nor the combined model explained even half of the variability in log spawning success of northern anchovy (Table 5). Although the model incorporating contaminants had somewhat

### Table 5

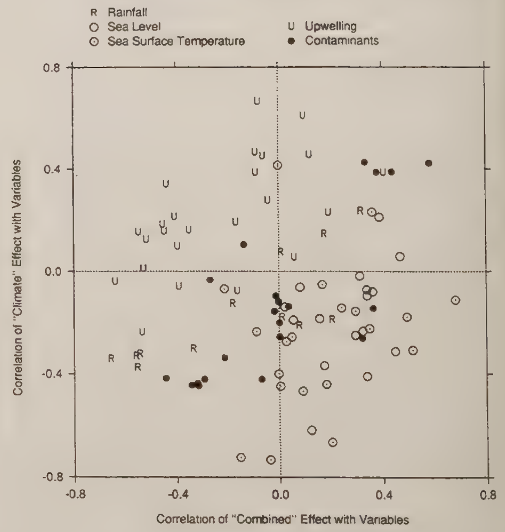
Summary results of regression models of logarithm of recruits per spawner for three coastal pelagic fish stocks off southern California. Predictor variables were parent stock size ($P$) and either principal components ($W_i$, $i$=1, ..., 10) of climate data (models denoted ○) or principal components ($C_i$, $i$=1, ..., 10) of climate data and data on contaminant loadings (models denoted ●). Each model also included an intercept. Variable selection used an all-subsets algorithm with the $C_p$ statistic; thus models may include variables not significant at $P<0.05$, and all $P$ values are considered nominal.

| Variables included in model (with sign of coefficient) and nominal probabilities of $t$-statistics for $H_0$: coefficient = 0. | df of model, error | $F$ statistic | Nominal Prob > $F$ | $R^2$ |
|---|---|---|---|---|
| **Northern anchovy *Engraulis mordax*** | | | | |
| ○ $-P$, 0.025; $-W_5$, 0.13 | 2, 15 | 4.20 | 0.036 | 0.36 |
| ● $-P$, 0.17; $-C_5$, 0.087; $-C_7$, 0.13 | 3, 14 | 4.14 | 0.027 | 0.47 |
| **Pacific sardine *Sardinops sagax*** | | | | |
| ○ $-W_5$, 0.030 | 1, 15 | 5.77 | 0.030 | 0.28 |
| ● $-P$, 0.0004; $-C_1$, 0.0001; $-C_5$, 0.002; $+C_{10}$, 0.002 | 4, 12 | 14.4 | 0.0002 | 0.47 |
| **Chub mackerel *Scomber japonicus*** | | | | |
| ○ $-P$, 0.0001; $-W_2$, 0.015; $+W_4$, 0.021; $+W_6$, 0.008; $-W_7$, 0.023; $-W_{10}$, 0.09 | 6, 23 | 6.74 | 0.0003 | 0.64 |
| ● $-P$, 0.0003; $+C_3$, 0.094; $-C_4$, 0.004 | 3, 26 | 8.11 | 0.0006 | 0.48 |

higher $R^2$ and nominal significance level* than the model including only climate effects, it is impossible to attribute this difference to the effects of contaminants on recruitment. Given the small sample size and relatively small difference in fit, it seems more logical to attribute it to chance.

The two models of anchovy spawning success can be compared by plotting the correlations of the two corresponding explanatory effects with the original explanatory variables (Fig. 4). For some variables (e.g., those related to rainfall), correlations are similar between models; however, many other variables fall into the second and fourth quadrants of the plane, meaning that they are positively associated with spawning success in one model and negatively associated in the other. For example, the two models assign opposite signs to the influence of most upwelling variables. Based on this inconsistent pattern of correlations (Fig. 4) and the lack of nominally significant parameters (except for the stock-size parameters) in Table 5, we conclude that these models identify neither climate- nor contaminant-related variability in the spawning success of this stock.

Indeed, the major determinants of anchovy recruitment strength remain to be discovered. Smith (1985) speculated that recruitment might be controlled in late-larval stages through "plasticity of the interaction between growth rate and survival." Peterman & Bradford (1987) detected a decrease in larval survival associated with episodes of high wind speed; however, Peterman et al. (1988) did not detect significant corre-



### Figure 4

Comparison of two regression models of logarithm of spawning success (recruits/spawner) of northern anchovy *Engraulis mordax* stock off southern California. Models include effects of stock size and environment. Coordinates of a point are the correlations of the models' explanatory effects (see text) with an explanatory variable. For legibility, only category of variable (point) is indicated. Vertical axis: correlations with model estimated on climate data. Horizontal axis: correlations with model estimated on combined climate and contaminant data. Points in first and third quadrants of plane indicate agreement between models as to a variable's effect; points in other quadrants indicate disagreement. Plot suggests that neither model offers a clear explanation of anchovy spawning success.

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*To emphasize the impossibility of determining true significance levels, reported significance levels are denoted "nominal."

lation between abundance of larvae and of later early stages or between larval abundance and subsequent recruitment. Because our explanatory data do not include wind speed, we were unable to address this specific question. Cury & Roy (1989) demonstrated that spawning success in coastal pelagic fishes responds nonlinearly to upwelling, but our linearized model could not include this possible relationship.

Methot (1989) has shown that the age of maturity in northern anchovy increases from 1 to 2 when temperatures are below average. Our data already account for this effect, because the spawning-stock estimates of Methot (1989) incorporate this effect of temperature.

The only other likely determinant of anchovy recruitment is spawner abundance itself. This is a straightforward phenomenon in which very low abundance produces very low recruitment. Our stock-recruitment plot (Fig. 1c) does not illustrate this phenomenon; however, the plot begins after the lower abundances of the 1950s, when the effect would have been most pronounced.

### Pacific sardine

As in the northern anchovy, the spawning biomass of Pacific sardine depends strongly upon immediately-preceding recruitments, with peaks in recruitment preceding peaks in spawning biomass by about 2 yr (Fig. 2a). Interpretation of the stock-recruitment plot (Fig. 2c) is problematic: If the 2 yr of highest spawning biomass (1949 and 1950) are disregarded, the plot appears biphasic, with small spawning biomasses producing small recruitments and large biomasses producing large recruitments. But if all years are included, recruitment appears to be density-dependent (or strongly influenced by external factors). The stock-size effect estimated by the model with climate effects was not significant ($P=0.66$); we refit the model without a stock-size effect (Table 5), reducing the $R^2$ by only 1%. The model with combined climate and contaminant effects identified a statistically significant stock-size effect with the correct sign for compensation (Table 5). This model also fit the data much better.

The two models give quite different pictures of the climatic effects associated with good spawning success in this Pacific sardine stock (Fig. 5). Correlations with rainfall-related signals were mostly negative for both models. Sea level and sea-surface temperatures were estimated to have mostly negative effects in the climate model, but many of these were estimated as positive in the combined model. Correlations with upwelling variables were all positive in the climate model, but were mixed in the combined model.

Most correlations with contaminant variables were negative in both models. In the climate model, correlations ranged from ~0.25 to –0.50. In the model with combined effects, the correlations ranged from ~ –0.25 to ~ –0.95. These strong and consistently negative correlations are consistent with the hypothesis that contaminants affected the dynamics of the Pacific sardine stock, perhaps contributing to its collapse.

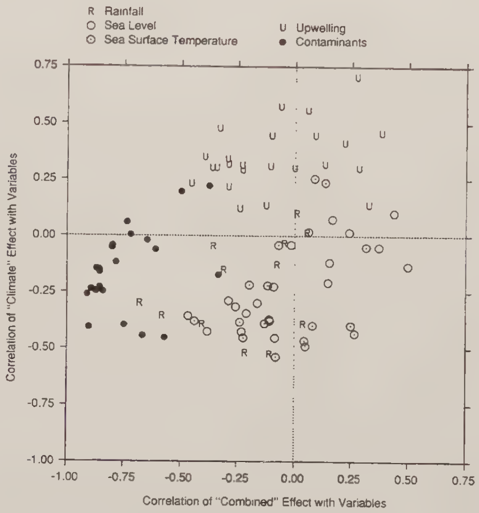

**Figure 5**

Comparison of two regression models of logarithm of spawning success (recruits/spawner) of Pacific sardine *Sardinops sagax* stock off southern California. Models include effects of stock size and environment. Coordinates of a point are the correlations of the models' explanatory effects (see text) with an explanatory variable. For legibility, only category of variable (point) is indicated. Vertical axis: correlations with model estimated on climate data. Horizontal axis: correlations with model estimated on combined climate and contaminant data. Points in first and third quadrants of plane indicate agreement between models as to a variable's effect; points in other quadrants indicate disagreement. Stronger negative correlations of "combined" model suggest that contaminants have had a negative effect.

### Chub mackerel

The models of chub mackerel spawning success included statistically-significant, compensatory stock-size parameters of similar magnitude (Table 5). Compensation has been demonstrated in previous analyses of this stock (Parrish & MacCall 1978, MacCall et al. 1985), and is apparent in Fig. 3b.

Including contaminant variables added little to the model. The climate model had lower MSE than the combined model, and its nominal significance level was more extreme (Table 5). One is left with the impression that adding the contaminant variables merely muddied the picture.

The two models give similar pictures of the forces that appear to be associated with variability in spawning success of chub mackerel (Fig. 6). We consider the climate variables first. Both models showed moderate-to-strong positive correlations of spawning success with sea-surface temperature early in the year, moderate-to-positive correlations with sea level early in the year, and weak-to-moderate correlations with upwelling later in the year. Correlations with rainfall-related variables were weak.

The models were also similar in correlations with contaminant variables. Correlations with metal loadings were weak-to-moderate, but of different signs for different metals; this suggests chance (noncausal) correlations. Much of the signal in the metal loadings occurred in the late 1960s and beyond, when the chub mackerel stock was declining from overfishing and then recovering (MacCall et al. 1985); this coincidence could have induced noncausal statistical correlations. Correlations with organochlorines were negative. In interpreting this, it is relevant that spawning success in chub mackerel is highly autocorrelated and appears periodic (Fig. 3b). The organochlorine abundances are also very highly autocorrelated, usually consisting of a single peak. This could easily lead to correlations like those observed, even if the observed contaminant levels did not affect spawning success.

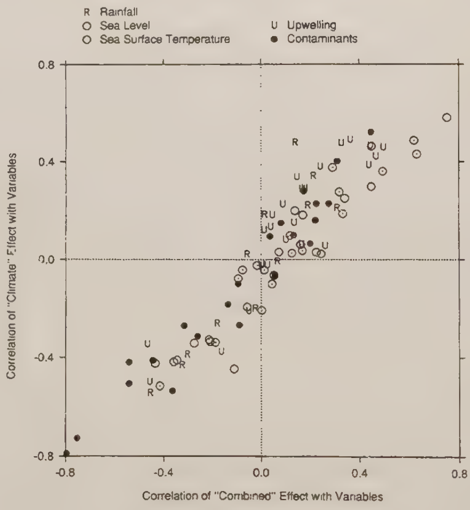

**Figure 6**

Comparison of two regression models of logarithm of spawning success (recruits/spawner) of chub mackerel *Scomber japonicus* stock off southern California. Models include effects of stock size and environment. Coordinates of a point are the correlations of the models' explanatory effects (see text) with an explanatory variable. For legibility, only category of variable (point) is indicated. Vertical axis: correlations with model estimated on climate data. Horizontal axis: correlations with model estimated on combined climate and contaminant data. Points in first and third quadrants of plane indicate agreement between models as to a variable's effect; points in other quadrants indicate disagreement. Strong agreement between models suggests that addition of contaminant data adds little to this model.

Although several contaminants correlate very highly with spawning success, the correlation patterns are nearly identical for the two models, one of which contains no information on contaminants. We interpret this to indicate that any contaminant effects are indistinguishable from effects of climate variables that fluctuate similarly over time. The strong agreement between the two models also suggests that recruitment-based contaminant analyses of this stock may be exceptionally prone to Type-II error, i.e., failure to detect any contaminant effects that might actually be present.

Parrish & MacCall (1978) also explored the effects of climate on chub mackerel spawning success, but comparison of this work and theirs is difficult for two reasons. Parrish & MacCall (1978) examined many explanatory variables not included in this study. In addition, changes in the estimated maturity schedule and the VPA-based stock and recruitment information (Prager & MacCall 1988) have resulted in a markedly different, as well as considerably extended, stock and recruitment series. Nonetheless, many of our estimated correlations agree with those of Parrish & MacCall (e.g., the positive effects of sea-surface temperature in the south, and the upwelling index at 30°N). Whereas Parrish & MacCall found that spawning success had a negative correlation to sea level at La Jolla, we estimated positive correlations with sea level at La Jolla and Los Angeles from January to June and independence in the later months.

## Statistical evaluation of contaminant effects

In a preceding section we developed three statistical criteria for admission of possible contaminant effects. The sign test required 12 negative correlations between 16 "deleterious" contaminant variables and the explanatory effect of a model using the combined explanatory data. Correlations for models of all three stocks were mostly negative. Models of northern anchovy (Fig. 5) and chub mackerel (Fig. 6) each contained 11 negative correlations, but neither result was sufficient to reject the null hypothesis. However, all 16 correlations were negative for the Pacific sardine (Table 6).

Regression coefficients were significant in models of Pacific sardine and chub mackerel. The model of northern anchovy spawning success fit relatively poorly (Table 5), and although the overall model was statistically significant, the individual regression coefficients were not.

According to the Schwarz criterion *S*, the models using combined data were marginally preferable to the models using climate data for chub mackerel and northern anchovy (*S* increased in the third significant figure). For sardine, the combined model was strongly preferable (*S* in ratio 2:1). Even allowing that the chub mackerel and northern anchovy models passed this test, the only stock to pass all three tests for suspicion of contaminant effects was the Pacific sardine.

## Discussion

A somewhat similar biostatistical study was conducted by Martin Marietta Environmental Systems to examine possible effects of contaminants on fishes in five estuaries of the U.S. Atlantic coast, with emphasis on the Hudson-Raritan basin (Summers et al. 1985, 1987). The study used a categorical regression model of historical landings (Rose et al. 1986); the autoregressive model did not attempt biological or demographic realism. After accounting for the effects of hydrographic conditions and previous stock sizes, Summers et al. (1987) detected correlations related to contaminant variables including dissolved oxygen, dredging, and biochemical oxygen demand. The study concluded that there were consistent patterns of anthropogenic influences among similar stocks across different estuaries. In a second categorical regression study, Summers et al. (1990), while expressing some reservations about ultimate causes, concluded that sewage loadings have had a negative effect on white bass *Morone americana* production in the Choptank River, Maryland.

The present study was not undertaken with the expectation of finding clear evidence that contaminants affected fish stocks, nor clear evidence to the contrary. We knew of many reasons that contaminant effects might be difficult to detect, including major theoretical and practical difficulties in the data, shortcomings in biological knowledge, and the limitations of available statistical methodology (for details, see Appendix). As expected, we failed to detect contaminant effects on anchovy or chub mackerel, although we are unable to state whether this reflects a lack of such effects or merely low statistical power. In contrast, the results for Pacific sardine suggest that contaminant stress, at a time of severe overfishing, contributed to the decline and collapse of this stock. Partly because we searched for the best among many possible models, we cannot attach any level of statistical certainty to this suggestion. Our search selected a model of high explanatory power ($R^2$=83%) in which contaminants were strongly represented, and that, we believe, makes a strong case for further research into the question. Important areas of research would include investigating how such a model of historical events, not formulated a priori, can be statistically validated (or invalidated); which individual contaminants may have contributed to the stock collapse; and by what mechanisms contaminants may have played a role in the decline of Pacific sardine.

An alternative hypothesis about Pacific sardine is that the true spawning-success relationship is depensatory rather than linear, and thus depensation, rather than exogenous influences, mediated the decline of the stock. Consistent with this hypothesis, the stock-size component of our model (Fig. 7a) fits the observed spawning-success data quite well until the mid-1950s (years of very low population size) when the stock-size component predicts higher spawning success than was observed. To examine this alternative hypothesis in more detail, we fit spawning-success models using the following variant of the gamma function:

**Table 6**

Statistical criteria used to screen models of spawning success of three coastal pelagic fish stocks off southern California. As predictors, models used parent stock-size and principal components derived from measures of climate and of contaminant loadings. Models were required to meet all three criteria in this table before being considered suggestive of contaminant influences on spawning success.

| Statistical criterion | Fish stock<br>Northern anchovy | <br>Pacific sardine | <br>Chub mackerel |
|---|---|---|---|
| Number of significant negative correlations with contaminants thought to be deleterious (12 required). | 11 | 16 | 11 |
| Significance of coefficients in model that included contaminants. | no | yes | yes |
| Improved fit of model including contaminants, compared with model including only climate. (Improvement judged by Schwarz criterion.) | yes | yes | yes |

$$\log(R/P) = a + \gamma \ln P + bP + \sum_{i=1}^{m} \theta_i x_i + \varepsilon. \qquad (4)$$

This differs from our original model, Eq. 3, only in including the term containing the estimated parameter $\gamma$. When $\gamma = 0$, this term drops out and the model is equivalent to Eq. 3. When $\gamma < 0$, the model is more strongly compensatory than Eq. 3; when $\gamma > 0$, the model is depensatory. In results of fitting this model, the depensatory effect was estimated as significant only in the absence of climate or combined variables ($\hat{\gamma}$= 1.57, $P < 0.025$ for a one-sided $t$-test). With the introduction of climate variables, the depensatory effect became smaller and not statistically significant ($\hat{\gamma}$=1.02, $P < 0.19$); with the introduction of the combined variables, the depensatory effect disappeared ($\hat{\gamma}$= −0.53, the wrong sign for depensation). In the model with a depensatory parameter, correlations of the explanatory effect (summation term in Eq. 4) with contaminants were within 2% of those obtained from the model without the depensatory parameter. Of course, the correct specification of spawning-success relationships may be more complex than even Eq. 4. Nonetheless, these results indicate that a simple model including depensation cannot account for the observed decline in spawning success residual to stock-size effects. When this decline, as modeled by our combined variables (Fig. 7b), is combined with Ricker stock-size effects, the resulting model fits well the observed data on Pacific sardine (Fig. 7c).

Are there plausible mechanisms by which contaminants may have contributed to the decline of the sardine population? The high fat content of sardines, anchovy, and mackerel makes them likely to accumulate fat-soluble compounds such as the organochlorines listed in Table 2. It is known that DDT has caused widespread reproductive failures in birds, including those in this geographical area (Anderson et al. 1975). Also, fish have been observed to depurate PCBs by transferring them into eggs (Binder et al. 1984). Since the early stages of many fish species have exhibited reduced survival rates after exposure to toxic compounds (Weis & Weis 1989), plausible mechanisms do exist. The Pacific sardine stock was under severe overfishing pressure at the time of its collapse, and such pressure would increase its susceptibility to environmental stress. The possibility that contaminants may be implicated in the collapse of a major marine fishery is a novel and startling one.

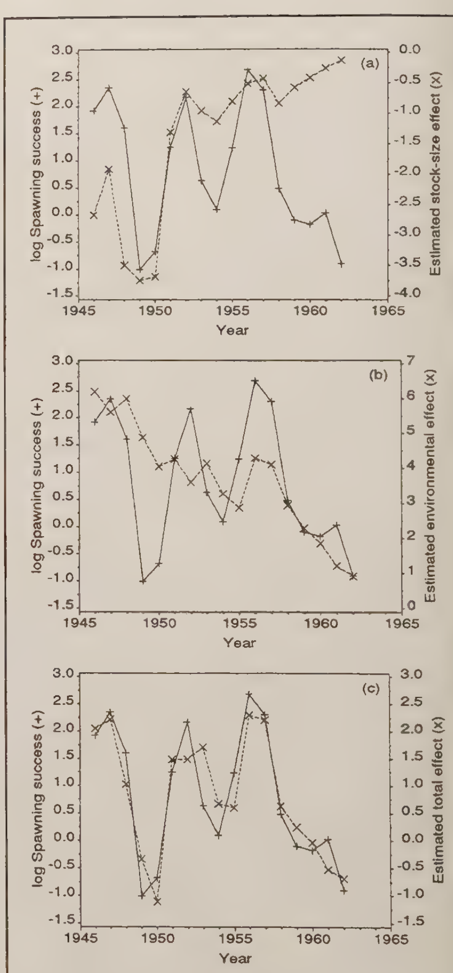

**Figure 7**

Components (dashed lines) of a model of spawning success (recruits/spawner) of Pacific sardine *Sardinops sagax* stock off southern California. Each panel also shows the observed spawning-success data (solid line) after logarithmic transform. **(a)** Model component associated with estimated stock-size (depensatory) parameter; **(b)** model component associated with estimated parameters corresponding to climate variability and contaminant loadings; **(c)** predicted values from full model (intercept plus stock-size and environmental effects). The environmental component is more influential in the mid-1950s and later, when contaminant loadings generally increased.

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## Appendix

We encountered many statistical difficulties and uncertainties in our biostatistical approach to detecting contaminant influences. Anyone attempting to interpret our results or to conduct a similar analysis should be cognizant of the following issues concerning data, biological understanding, and statistical methodology.

### Difficulties relating to the data

- imprecision in data on stock and recruitment;
- imprecision in measurements of physical (climatic) conditions;
- imprecision in measurements and reconstructions of contaminant loadings;
- lack of residence-time models for contaminants in the water column and sediments, necessitating the use of loading (influx) values, rather than estimated *in situ* concentrations;
- substantial environmental variability that cannot be modeled effectively, and that would thus become "noise";
- strong trends in some resource and contaminant histories that can produce ambiguous correlations between these quantities;
- time-series that are short by statistical standards, although long by comparison with others available;
- multicollinearity: similar patterns over time in different explanatory variables.

### Shortcomings in biological understanding

- only rudimentary knowledge of biological response to environmental variability and contaminants;
- poor models of environmental influences on larval production and recruitment;
- poor knowledge of spawning-at-age schedules, especially in light of increased evidence of multiple spawnings within seasons;
- little knowledge of natural mortality rates for most species;
- little or no knowledge of the true form of stock-recruitment relationships for most species.

### Problems with statistical methodology

- lack of methods to address the problem of errors-in-variables, except in the simplest cases;
- lack of methods to determine the statistical power of hypothesis tests; and
- lack of methods to identify conclusively a model with the optimum number of parameters, or, for that matter, the correct non-zero parameters;
- possible presence of nonlinear effects, but insufficient data to identify and estimate a nonlinear model.

Similar problems arise in diverse areas of biostatistical analysis of populations and ecosystems, including most studies conducted for fishery management.

We attempted to reduce the effects of collinearity among the explanatory variables by using principal-components analysis. Unfortunately, stock size was at times correlated to other variables. The inability to identify effects of individual climate or contaminant variates is an unavoidable result of collinearity. This problem was accentuated by autocorrelation in the explanatory data and in the stock and recruitment series. Time trends in several explanatory variables, including stock size, compounded the problem of multi-collinearity, as they can lead to spurious (noncausal) correlations.

Even after the principal-component analysis, the suite of possible explanatory variables was large. For parsimony, we chose subset models for each stock. As stated, it is nonetheless probable that our models contain specification error. There are three main forms of specification error: (1) omission of relevant variables or inclusion of irrelevant ones, (2) a wrong functional form for the model (e.g., quadratic response when linear is specified), and (3) changes in the true parameters over time. Consequences of specification error can include biased parameter estimates and biased estimates of variance (Kennedy 1979), which in turn can lead to reduced statistical power. Using principal components, which are biologically arbitrary combinations of variables, may conceivably contribute to specification error (including errors in variables, as defined below).

Most of the recruitment time-series derived from VPA were short and did not coincide exactly with the contaminant data series, themselves not exceptionally long. A major consequence of modeling with a small sample size is low statistical power.

Observation error in explanatory variables causes difficulties in OLS parameter estimates, including inconsistency and, in the bivariate linear case, bias towards zero (Theil 1971, Kennedy 1979). This is known in the field of econometrics as the "errors-in-variables" or "errors-in-predictors" problem, and is sometimes considered a special case of specification error (e.g., Theil 1971). It has been demonstrated that recruitment models used in fisheries are subject to this problem (Walters & Ludwig 1981, Goodyear & Christensen 1984). If one is interested only in a predictive model, the bias is not important. If the parameter estimates are the object, however—as in the present case—the bias is especially problematic because its direction and magnitude are known only in a few simple cases. By analogy to the results in bivariate linear regression, we suspect that coefficients of our regression models are biased towards zero. The estimated correlations with individual explanatory variates, including contaminants, may also be biased towards zero because of the smearing of the relationship by errors in the predictors.

Further complication is caused by the strong correlations between potential explanatory variables reflecting climate and those reflecting contaminant loadings (Prager & MacCall 1990, Table 6.1). A few examples are the correlations between annual dredging removals and total rainfall in San Diego ($r$=–0.32), PCBs loadings and July–August SST at San Luis Wharf ($r$=0.63), and lead loadings and May–June upwelling at 39°N, 122°W ($r$=0.79). This collinearity makes it nearly impossible to distinguish, by statistical means, the effects of climate from those of contaminants.

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# YELLOWFIN TUNA, DOLPHINS AND THE EASTERN TROPICAL PACIFIC FISHERY: IS IT SAFE?

Gary T. Sakagawa*

## INTRODUCTION

The controversy over tuna fishing and dolphin protection has gained international attention largely as a result of recent debates in the press on the United States' action to embargo yellowfin tuna from suppliers trading in tuna and having weak or no regulations to protect dolphins in the fishing process, and tuna canneries in the United States adopting a policy of processing only tuna caught with dolphin-safe techniques. This controversy has its roots in the eastern tropical Pacific (ETP), which is the region off Central and South America east of about 150° W longitude.

The tuna-dolphin controversy emerged in the 1960s with discovery that U.S. vessels were responsible for large numbers of dolphins killed incidentally to tuna fishing with purse seine nets in the ETP (Sakagawa 1991). This discovery generated intense debate and strong public support in the U.S. for protecting dolphins. Beginning in 1972, the U.S. government responded with a series of laws to protect dolphins and other marine mammals. This encouraged the U.S. tuna industry to develop dolphin-saving techniques and to use methods for preventing needless dolphin mortality in tuna purse seine fishing (Coe, Holts and Butler 1984). Significant reduction in dolphin mortality was realized by the U.S. fleet from these efforts (from 166,600 animals in 1975 to 1,004 animals in 1991). Unfortunately, the positive advances by the U.S. fleet were not matched by the growing non-U.S. fleet. Instead, total incidental mortality (all fleets combined) of dolphins remained high as the non-U.S. fleet expanded their fishing and contributed a greater share to the total incidental mortality. Environmentalists became frustrated with this setback, and resolved to expand the tunadolphin debate to the international arena.

My talk today will not be a review of pluses and minuses of the tuna-dolphin issue in tuna fishing, or a discussion of the legal, moral or ethical arguments of government and private actions to date on this issue. Such a presentation is best done by government administrators and other qualified experts. My purpose today is, instead, to (1) review the dynamics and statistical trends of the ETP fishery, and (2) project those trends to provide a probable scenario of the future fishery.

I begin with first noting that yellowfin tuna, *Thunnus albacares*, is the only tuna species that consistently forms a natural symbiotic relationship with dolphins, mainly of the genus *Stenella*, in the ETP. The relationship is probably related to optimizing foraging strategy (Au and Perryman 1985) and is often referred to as a "bond." This bond is not easily broken. When an aggregation of yellowfin tuna and dolphins is encountered and frightened, the dolphins flee with the yellowfin tuna following directly below and close behind. Purse seine fishermen in the ETP use this bond by encircling the tuna-dolphin complex, because they are aware that capturing the dolphins is the only procedure to insure capture of the tuna as well. Techniques are then used to remove the dolphins alive from the net in order to land the valuable tuna. However, when the techniques are not used properly or diligently, some dolphins die in the net or are badly injured and die eventually after release.

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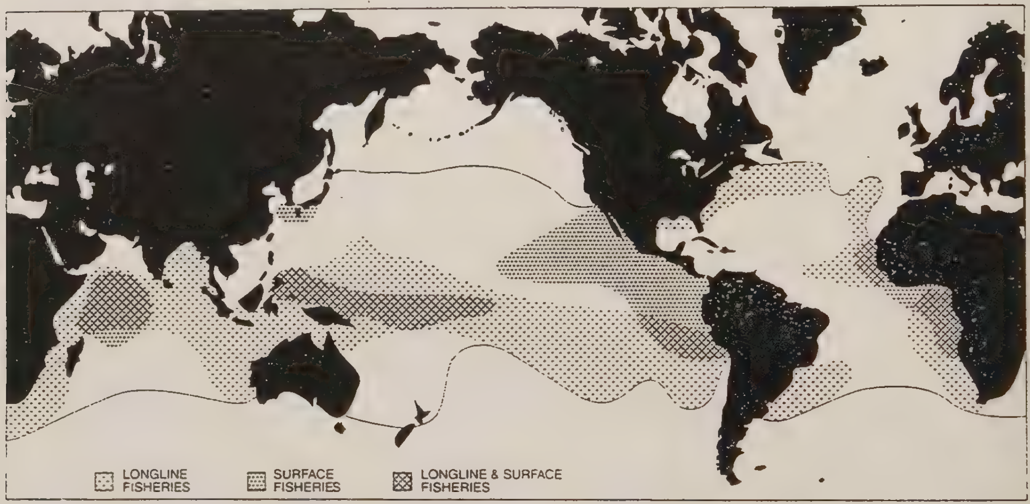
## YELLOWFIN TUNA THE TARGET SPECIES

Yellowfin tuna is found over a wide range in the Pacific Ocean from off Japan to New Zealand in the west and from off the U.S. to Chile in the east (Figure 1). Fishing for this species is conducted throughout this range with various fishing gears, but only selected tropical regions of the range appear to be suitable for large-scale surface fishing with purse seine gear. One of those regions is the ETP.

FIGURE 1 **Global geographic ranges and fishing areas for yellowfin tuna.**

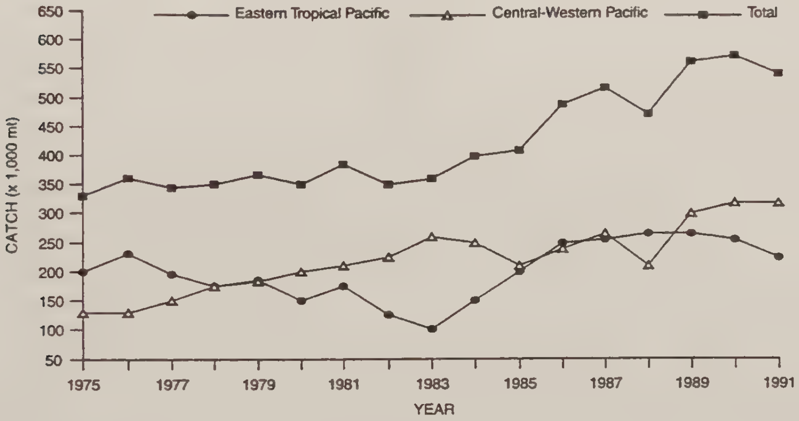


In the ETP, the purse seine fishery targets yellowfin tuna, which is landed mainly for the canned tuna market. The catch is currently (1990-91) at a high level — 210,000 to 280,000 t per year (Figure 2) — and the stock is in good condition. In the late 1970s, this was not the case. The stock was being overfished and was on a decline after peaking in the early 1970s. The stock was unable to sustain profitable catch rates and catches for U.S. vessels, so vessels began leaving the region for the western Pacific. The exodus was initially a few vessels each year until 1983 when a substantial number switched from the ETP to the western Pacific. Since then, the U.S. tropical tuna purse seine fleet has shrunk to less than 10 vessels in the ETP, with about 45 vessels operating in the western Pacific (Sakagawa 1991). Simultaneously during the exodus, new vessels were being added to the non-U.S. component of the ETP fleet and operated successfully through government support. The net result was a small decline in the total number (all fleets) of large purse seiners in the ETP fishery — about 24% decline in number of large purse seiners between 1976 (170 vessels) and 1990 (130 vessels).

The large exodus in 1983 is particularly significant because it occurred during the period of the strongest El Niño phenomenon of the century. The phenomenon modified ocean currents and affected the global climate. The phenomenon also significantly affected the catch of yellowfin tuna in the entire Pacific Ocean (Figure 2). Before 1983, the total Pacific catch of yellowfin tuna was relatively stable at about 350,000 t annually.

During the 1982-83 El Niño availability of yellowfin tuna in the ETP was significantly reduced, and in the western Pacific, significantly increased. The catch in the ETP plummeted and increased in the western Pacific. Since then catches recovered and increased to new records in the ETP and continued to increase in the western Pacific. For the entire Pacific, the current catch is approximately 600,000 t per annum.

FIGURE 2 **Total catch of yellowfin tuna from eastern and western regions of the Pacific Ocean, 1977-91.**

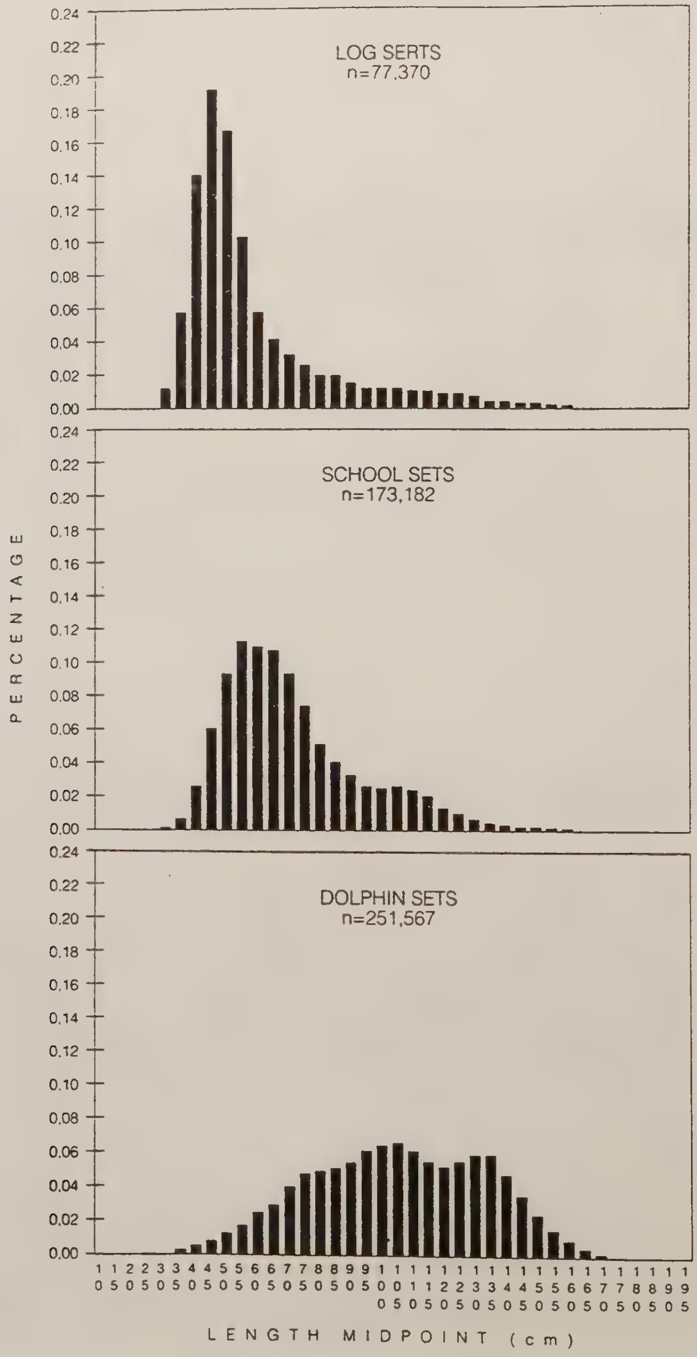


Some researchers believe that the 1982-83 El Niño event created a permanent shift in the environmental regime that allowed for increased production and subsequent high yield of yellowfin tuna in the Pacific Ocean. The hypothesis is that the change brought about improved survival of young and increased the abundance of yellowfin tuna available to the fishery — about 30% higher than levels during the early 1970s and 110% higher than levels during the overfishing years of the late 1970s in the ETP (IATTC 1991). Other researchers hypothesize that if a regime change has occurred and abundance has increased as a result, that this is only a temporary situation and the regime will soon revert to the original pre-1982-83 El Nino state. With this hypothesis, yellowfin tuna abundance will return to lower levels. If so, then the current yield of 600,000 t annually appears to be unsustainable and the sustainable yield might be closer to the 350,000 t level recorded before the 1982-83 El Niño event. No one knows which one of these hypotheses is correct and researchers continue to work on this matter.

## DOLPHINS: INCIDENTAL SPECIES TAKEN IN THE FISHERY

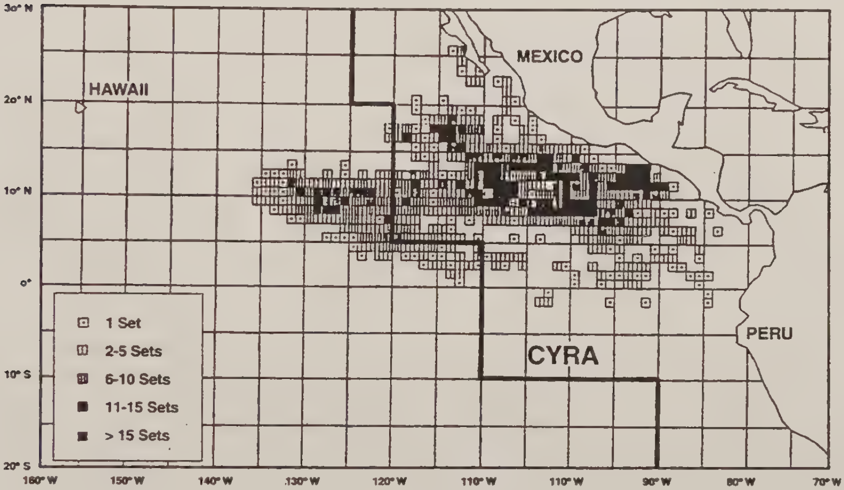
In the ETP tuna fishery, virtually the entire catch of yellowfin tuna is made with purse seine gear and the major portion is caught with dolphins. On the average, for every 3 t of yellowfin tuna caught in the ETP purse seine fishery, 2 t are caught with dolphin-associated schools and 1 t with flotsam-associated or on free-swimming schools. Yellowfin tuna caught in dolphin-associated schools are generally large fish, but sizes caught vary and overlap those for other school types (Figure 3). Fishermen prefer the

FIGURE 3 **Average (1974-90) length-frequency distribution of yellowfin tuna by school or set type from the eastern tropical Pacific. (From: Hall, Lennert and Arenas 1992)**



large yellowfin tuna because they are worth more than smaller yellowfin tuna (e.g., exvessel US$860/t for about 20 kg fish versus US$735/t for 3 kg fish in March 1992). Also, catch rates for dolphin-associated schools, which yield the large yellowfin tuna, tend to be high, although in some years, flotsam-associated schools produce the highest catch rates (Greenblatt 1979).

FIGURE 4 **Location and number of sets made on tuna-dolphin schools by U.S. purse-seiners in the eastern tropical Pacific Ocean in 1987, and the boundary of the Inter-American Tropical Tuna Commission's yellowfin tuna regulatory area (CYRA). (From: Sakagawa 1991)**

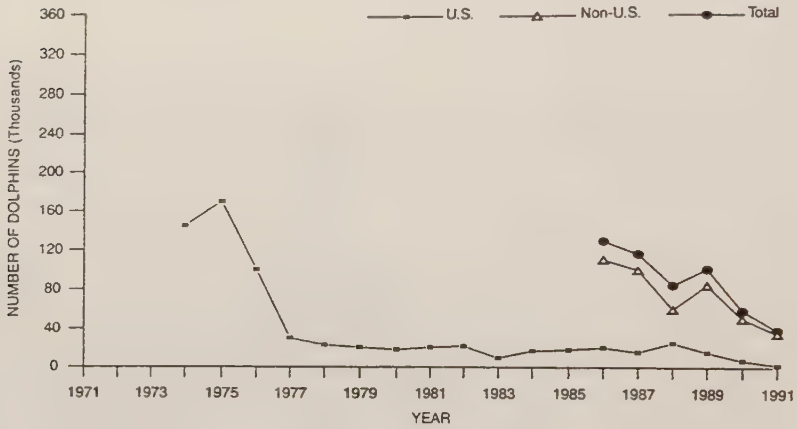


Four species of dolphins (spotted dolphin, *S. attenuata*; spinner dolphin, *S. longirostris*; striped dolphin, *S. coeruleoalba*; and common dolphin, *Delphinus delphis*) consisting of 9 currently recognized stocks are principally involved in the fishery. Each species-stock has its unique geographic range (Perrin, et al. 1975), but all have ranges that fall largely in the ETP purse seine fishing area (Figure 4). By far the most important species-stock is the northern spotted dolphin.

In the 1960s and early 1970s when dolphin-saving techniques were not fully known and used, 170,000 to 500,000 dolphins were killed by the fishery each year (Figure 5). With development and wide-use of dolphin-saving gear and procedures by the U.S. fleet, the incidental kill was reduced significantly in the late 1970s and maintained at a low level for this fleet (Sakagawa 1991). The non-U.S. part of the fishery, on the other hand, increased in size and was less effective in saving dolphins; consequently, total dolphin mortality for the fishery remained high (about 100,000 animals per year) until at least 1987. Since then, wider use of dolphin-saving gear and procedures by the non-U.S. fleet has been implemented and the total incidental kill has begun to decrease. The total in 1991 was 27,000 dolphins. A further reduction is anticipated in 1992 (M. Hall, IATTC, pers. communication).

Dolphin populations have been affected adversely by the ETP purse seine fishery and are currently at lower levels than existed before the purse seine fishery expanded. The

FIGURE 5 **Estimated number of dolphins killed by U.S. and non-U.S. purse-seine vessels participating in the eastern tropical Pacific tuna fishery. Although sampling by observers began in 1971 for the U.S.fleet and in 1983 for the non-U.S. fleet, coverage was not adequate until 1974 and**



greatest reductions in the populations occurred in the 1960s and early 1970s (Smith 1983). Available data indicate population declines of as much as 50% between 1970 and 1980 (IATTC 1992). Since about 1980, the populations have remained stable with no clear trend. Recovery to higher levels that existed before 1980 is not expected to be rapid, despite significant reductions in incidental mortality, because the animals have a low birth rate and significant reductions in incidental mortality have occurred only recently. For 1986-90, the population of northern offshore spotted dolphin was estimated to average 1.5 million animals (Wade and Gerrodette 1992).

## THE FUTURE FISHERY

What is the outlook for the ETP fishery? Predicting the future of the ETP fishery would be largely speculative given uncertainties with government actions/reactions to possible international dolphin regulations and uncertainties in economic forces affecting the tuna industry. However, actions to date have produced trends that will probably continue into the near future and dominate events despite the uncertainties. Assuming that the trends will continue, I propose two probable scenarios for the future ETP fishery.

The first scenario builds on the following current trends: yellowfin tuna abundance in the ETP will continue to be at record high levels; dolphin-saving technology will be more widely and diligently used by all purse seine fleets in the ETP; dolphin-safe labeling of canned tuna will continue to gain support; and the global catch of tropical tunas will continue to increase. Assuming these trends continue, the ETP fishery will operate for the near-term at a status quo of high yellowfin tuna production, but with increased cost for assuring that incidental dolphin mortality is reduced to levels approaching zero mortality. With time, however, yellowfin tuna production will decline as fishing on dolphin-associated schools taper off in response to consumer preference for dolphin-safe tuna products.

The key to this scenario is increased consumer support for dolphin protection and continued high production of tropical tunas in fishing areas outside the ETP where there is no serious tuna-dolphin problem. Production of primarily skipjack tuna, *Katsuwonus pelamis*, but also yellowfin tuna as well, from areas other than the ETP has been increasing in recent years. This has lessened the dependence of major processors on ETP production for raw material and has weakened the role of ETP production to set international raw material prices. For example, yellowfin tuna caught in the ETP was once the mainstay for the large U.S. canned tuna market and was the leader in setting global raw tuna prices. In 1990 less than 10,000 t of ETP yellowfin tuna entered the U.S. market (about 690,000 t (Peckham 1992)) and raw material prices were largely set by production in other fisheries, e.g. western Pacific Ocean and Indian Ocean. Currently, the catch of yellowfin tuna associated with dolphins from the ETP make up only about 10% of the total world supply of raw material for the "light meat" canning market. Consequently, the price to consumers of a can of "dolphin-safe" tuna has been competitive to a can of "not dolphin-safe" tuna and skipjack tuna has become the major ingredient for the light meat pack.

As consumer awareness of the tuna-dolphin issue increases and product prices remain competitive, preference for dolphin-safe canned tuna will grow. More processors will join the movement to reduce or discontinue canning of ETP yellowfin tuna caught in association with dolphins in order to maintain market share. With time, fewer markets will be available for producers of ETP yellowfin tuna caught in association with dolphins. Fishing on dolphin-associated schools will decline and incidental dolphin mortality will likewise decrease to very low levels.

The second scenario builds on the recent movement to outlaw completely purse seine fishing on tuna-dolphin schools in the ETP and on conditions listed for scenario 1, i.e., yellowfin tuna abundance in the ETP remaining at high level, dolphin-safe canned tuna gaining in popularity, and global catch of tropical tunas increasing. This scenario predicts an immediate dislocation of vessels in the ETP fishery and a resulting decrease of the ETP yellowfin tuna catch. The experience of the U.S. fleet can serve as an example. In 1990, processors in the U.S. adopted a policy of not buying or selling tuna caught in association with dolphins. Because the majority of the U.S. fleet depended solely on the U.S. processors, many were unable to market their catch or find an alternative to remain in the fishery. Consequently, there was a large dislocation of vessels and significant reduction in the catch.

In the ETP, there are no readily available alternatives to fishing on tuna-dolphin schools that equal the high catch rate (IATTC 1992) and high value of the catch. Furthermore, the availability of non-dolphin associated schools, i.e. flotsam-associated and free-swimming, is largely centered within the jurisdiction of the ETP coastal nations (Joseph and Greenough 1979). The nations do not have a uniform policy to allow all vessels easy and at-reasonable-cost access to their jurisdiction. Consequently, many of the vessels in the current fishery cannot gain full access to the areas of non-dolphin associated schools and will have little choice except to stop fishing or move completely out of the fishery, if tuna-dolphin fishing is prohibited. The catch of yellowfin tuna will hence decline. The IATTC (1992) estimates that the catch will decline to about 150,000 t Yield per recruit will likewise decline to about 2.0 kg, as a result of increased small fish being caught (Figure 3). The high recruitment of recent years (1988-90 average of 95 million age 1 fish) to the fishery, however, is more than adequate to sustain a catch of 150,000 t annually, at low yield per recruit, and to maintain a healthy population.
For each of these scenarios, the effect on the populations, both yellowfin tuna and dolphins is favorable. The populations will be under less fishing pressure, subjected to less incidental kills or catch, and will be under less of a threat of depletion owing to fishing.

The serious impacts, however, will be on the fishery. The fishery for yellowfin tuna will shrink and be smaller over the long term with scenario 1 and almost immediately with scenario 2. Efforts to develop alternative fishing strategies for purse seine vessels, e.g. artificial drifting devices to attract fish and new fish locating devices (IATTC 1992), have started in earnest only recently and will take time to prove their profitability as a substitute. They will most likely not be ready in sufficient time to mitigate the impact. Consequently, the key issues emerging from these scenarios are not ones of the ETP resource, but challenges in dealing with the dislocation of a large segment of the ETP fleet and with the shortfall of about 100,000 t per year of yellowfin tuna to the global processing sector. How these issues are handled will affect not only the ETP fishery, but tropical tuna fisheries and stocks in other parts of the world as well. It is crucial, therefore, that the challenges be addressed with global considerations as well as ETP considerations.

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# Population Field Theory with Applications to Tag Analysis and Fishery Modeling: the Empirical Green Function

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Salvadó, C.A.M. 1993. Population field theory with applications to tag analysis and fishery modeling: the empirical Green function. Can. J. Fish. Aquat. Sci. 50: 2491–2512.

A theoretical framework is proposed for analyzing fish movement and modeling the associated dynamics using tagging data. When tagged fish are released in an area small compared with the domain of the fish population and over a period short compared with the time they take to disperse throughout their domain, the pattern of movement approximates a point-source solution of the underlying population dynamics. A method of point sources (Green functions) is invoked for representing the solution of the tagged and untagged fish field equations (partial differential equations) in terms of integral equations. As an approximate representation of a tagging experiment, the Green function is interpreted as the probability density of survival and movement from point to point in space–time. The Green functions are constructed empirically using one parameter, catchability, as the ratio of population density of tagged fish divided by the number of tagged fish released. The number of tagging experiments necessary to characterize the population is dictated by the dependence of catchability on space–time. The moments of the Green function are used to calculate model parameters and lead to the identification of a closed form expression for the transition probability densities of the model assumed.

Un plan de travail théorique est proposé pour analyser les déplacements des poissons et modéliser la dynamique connexe au moyen de données de marquage. Lorsque des poissons marqués sont relâchés dans une zone de faibles dimensions par rapport au domaine occupée par la population de poissons et sur une courte période par rapport au temps de dispersion nécessaire dans leur domaine, le profil de déplacement correspond à peu près à une solution de source ponctuelle de la dynamique des populations sous-jacente. Une méthode de sources ponctuelles (fonction de Green) est retenue pour représenter la solution des équations de mouvement des poissons marqués et non marqués (équations aux dérivées partielles) en fonction d'équation intégrales. À titre de représentation approximative d'une expérience de marquage, la fonction de Green est interprétée comme la densité de probabilité de la survie et du déplacement d'un point à l'autre dans l'espace et dans le temps. Les fonctions de Green sont établies de façon empirique à l'aide d'un paramètre, la vulnérabilité, qui correspond au rapport entre la densité de population des poissons marqués divisée par le nombre de poissons marqués relâchés. Le nombre d'expériences de marquage nécessaires pour caractériser la population est dicté par la dépendance de la vulnérabilité à l'égard du temps et de l'espace. Les moments de la fonction de Green sont utilisés pour calculer les paramètres du modèle et permettent l'établissement d'une expression fermée des densités de la probabilité de transition du modèle hypothétique.

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## 1. Introduction

Considerable effort has been devoted to understanding animal movement patterns (Okubo 1980; Murray 1989). In particular, the study of fish movement patterns by the use of tagging experiments has been reviewed by Hilborn (1990), who discussed recent studies on the subject (Bayliff 1979; Ishii 1979; Sibert 1984; Hunter et al. 1986; Kleiber et al. 1987). These studies require the assumption of a model (a partial differential equation, or, in general, a field equation) parameterized in such ways so that it accommodates the movement of tagged fish and the catch and natural death rate densities. The model parameters are typically evaluated by means of the tagging data and such extreme value principles as maximum likelihood estimators.

A field equation is also employed in the empirical method discussed here. It is one of great generality that can be stated simply as the inhomogeneous advection–diffusion equation (Okubo 1980) with mortality for dilute populations with spatially and temporally varying coefficients. The empirical method that will be exposed in this work is a one-parameter model and is adequate for answering the question on fisheries interaction posed in Section 2. It is also the first step that would be taken to prepare the data for fitting a multiple parameter model.

In a typical tagging experiment, tagged fish are released over a time interval short in relation to the time they disperse throughout their domain and into an area small in relation to the domain of the population. Under these conditions, the release and recovery data from the experiment approximate a point-source solution of the field equations that represent the population dynamics of the fish. The method of solving inhomogeneous linear differential equations by use of their point-source solutions has been known for many years, and the subject is referred to as the method of Green functions (Feynman 1949; Courant and Hilbert 1953; Morse and Feshbach 1953; Bjorken and Drell

1964; Garabedian 1964; Feynman and Hibbs 1965; Byron and Fuller 1970; Gilbarg and Trudinger 1979). The Green function associated with a linear differential equation is the solution of the differential equation under the influence of a unit impulsive source at one point (i.e., a source of unit strength applied at one space–time point) and therefore is the point-source solution.

In general, if tagged fish were released at every space–time point, the subsequent recapture results would differ between points owing to uneven distributions of fishing effort in space–time. In addition, there may be other influences that affect the patterns of the point sources such as geographic (e.g., boundaries) and cyclic factors (e.g., seasonal, El Niño). Nevertheless, each of the release and recovery measures still represents a point-source solution of the field equations that describe the underlying fish dynamics and, therefore, in some manner must be approximately a Green function associated with the dynamics.

Apparently, Green functions have never been used in modeling tagged fish populations, the reason probably being that the use of the method of Green functions requires linearity, and fish population dynamics processes, such as recruitment, are thought to be nonlinear. By separating the linear and the nonlinear parts, and by considering the nonlinear portion as being part of the term that makes the field equation inhomogeneous, the method of Green functions becomes not only useful, but conceptually simple, in fish population modeling.

The following symbols are used:

$\mathscr{A}$ = domain of the population
$\mathbf{R}^2$ = infinite plane
$\partial\mathscr{A}$ = boundary of $\mathscr{A}$
$\mathbf{n}_\perp$ = unit vector normal to $\partial\mathscr{A}$ pointing outward
$\mathbf{R}$ = infinite line
$\partial\mathscr{A}_A$ = portion of $\partial\mathscr{A}$ on which population is absorbed
$\partial\mathscr{A}_R$ = portion of $\partial\mathscr{A}$ from which population is reflected
$\mathscr{A}_i$ = neighborhood of point $\mathbf{r}_i$ referred to as a cell
$n$ = number of nonoverlapping cells defined in $\mathscr{A}$
$\boldsymbol{i}, \boldsymbol{j}$ = unit vectors respectively in the $+x$ and $+y$ directions
$\{O_i: i = 1, 2, \ldots\}$ = set whose members are $O_1, O_2 \ldots$
$\in$ = member of
$\subseteq$ = subset or equal to
$\cup$ = union
$<$ = less than
$>$ = greater than
$\ll$ = much less than
$\gg$ = much greater than
$\leq$ = less than or equal to
$\geq$ = greater than or equal to
$\sim$ = similar to, of the same order of magnitude
$\mathbf{r} = x\mathbf{i} + y\mathbf{j}$ = position vector $\in \mathscr{A}$
$r = \sqrt{\mathbf{r}\cdot\mathbf{r}}$ = magnitude of vector $\mathbf{r}$
$\mathbf{r}_T = x_T\mathbf{i} + y_T\mathbf{j}$ = location of tag release $\in \mathscr{A}$
$t$ = time
$a$ = age
$t_T$ = time of tag release
$[t_i, t_f] = t_f - t_i$
$\mathscr{T}_I = [t_I, t]$
$\mathscr{T}_T = [t_T, t] \subseteq \mathscr{T}_I$
$\mathscr{T}_j = [t_j, t_{j+1}]$
$\mathscr{T}' = [t', t]$
$\mathscr{T}$ = interval of time of arbitrary length; a period
$m$ = number of intervals of time $\mathscr{T}_j$ into which $\mathscr{T}_I$ is subdivided
$e(\mathbf{r},t)$ = fishing effort density field
$c_T(\mathbf{r},t)$ = tagged fish catch density rate field
$c(\mathbf{r},t)$ = untagged fish catch density rate field
$p_T(\mathbf{r},t)$ = tagged fish population density field
$p(\mathbf{r},t)$ = untagged fish population density field
$dl$ = infinitesimal line element
$d^2\mathbf{r}$ = infinitesimal surface element = $dxdy$ in Cartesian coordinates
$\nabla$ = differential operator $\mathbf{i}\partial/\partial x + \mathbf{j}\partial/\partial y$
$\triangle = \nabla\cdot\nabla = \partial^2/\partial x^2 + \partial^2/\partial y^2$
$\mathbf{j}(\mathbf{r},t)$ = flux of $p$
$s(\mathbf{r},t)$ = source and/or sink density rate of field $p$
$d(\mathbf{r},t)$ = natural death density rate field
$m(\mathbf{r},t)$, $m(t)$ = natural death rate
$q(\mathbf{r},t)$ = catchability
$f(\mathbf{r},t)$ = fishing death rate field = $q(\mathbf{r},t)\, e(\mathbf{r},t)$
$z(\mathbf{r},t) = m(\mathbf{r},t) + f(\mathbf{r},t)$
$N_T(\mathbf{r}_T,t_T)$ = number of tagged fish released at space-time point $(\mathbf{r}_T,t_T)$
$N_R$ = number of tagged fish recaptured in the interval of time $\mathscr{T}_T$
$\mathscr{L}_0$ = spatial differential operator dependent on $f$
$\mathscr{L}$ = spatial differential operator independent of $f$
$\mathscr{N}(\mathbf{r}',\sigma^2)$ = two-dimensional normal distribution centered at $\mathbf{r}' = x'\mathbf{i} + y'\mathbf{j}$ and variance $\sigma^2$
$\delta(\mathbf{r} - \mathbf{r}') = \delta(x - x')\delta(y - y')$ = two-dimensional Dirac delta function which can be represented as $\lim_{\sigma\to 0} \mathscr{N}(\mathbf{r}',\sigma^2)$
$g_0(\mathbf{r},t|\mathbf{r}',t')$ = effort-dependent Green function, which represents the probability density that a fish will survive the movement to point $\mathbf{r}$ from point $\mathbf{r}'$ in the interval of time $\mathscr{T}'$ when fishing takes place during that time interval
$g(\mathbf{r},t|\mathbf{r}',t')$ = effort-independent Green function, which represents the probability density that a fish will survive the movement to point $\mathbf{r}$ from point $\mathbf{r}'$ in the interval of time $\mathscr{T}'$ if no fishing takes place during that time interval
$r(\mathbf{r},t)$ = recruitment density rate field
$u_0(\mathbf{r},t)$ = population density due to recruitment = superposed recruitment density rate field with the effort-dependent Green function $g_0$
$u(\mathbf{r},t)$ = population density due to recruitment = superposed recruitment density rate field with the effort-independent Green function $g$
$h(t - t')$ = Heaviside step function which can be represented as $dh(t - t')/dt = \delta(t - t')$
$\mathbf{v}(\mathbf{r},t)$, $\mathbf{v}(t) = v_x\mathbf{i} + v_y\mathbf{j}$ = drift velocity
$k(\mathbf{r},t)$, $k(t)$ = diffusivity
$\mathscr{E} = \{e(\mathbf{r}_i,t_j) : i = 1, 2, \ldots, n;\ j = 1, 2, \ldots, m + 1\}$ = set of effort density measurements
$\mathscr{C} = \{c(\mathbf{r}_i,t_j) : i = 1, 2, \ldots, n; j = 1, 2, \ldots, m + 1\}$ = set of catch density rate measurements of untagged fish
$\mathscr{C}_T(\mathbf{r}_k,t_l) = \{c_T(\mathbf{r}_i,t_j) : i = 1, 2, \ldots, n; j = l, l + 1, \ldots, m + 1\}$ = set of catch density rate measurements of tagged fish released in cell $\mathscr{A}_k$ in the interval of time $\mathscr{T}_l$.
$\mathscr{C}_T = \{\mathscr{C}_T(\mathbf{r}_s,t_{l+s-1}) : s = 1, 2, \ldots, n\}$ = set of catch density rate measurement of tagged fish for $n$ tagged fish releases in zones $\mathscr{A}_s$, correspondingly in the intervals of time $\mathscr{T}_{l+s-1}$ for $s = 1, 2, \ldots, n$.
$\mathscr{Q} = \{q(\mathbf{r}_s,t_{l+s-1}) : s = 1, 2, \ldots, n\}$ = set of catchabilities computed from tagging experiments in cells $\mathscr{A}_s$ correspondingly in the intervals of time $\mathscr{T}_{l+s-1}$ for $s = 1, 2, \ldots, n$
$\mathscr{R} = \{r(\mathbf{r}_i,t_j) : i = 1, 2, \ldots, n; j = l + n, l + n + 1, \ldots, m + 1\}$ =

set of recruitment density rates computed at $\mathcal{A}_i$ in the intervals of time $\mathcal{T}_j$ for $j = l + n, l + n + 1, \ldots, m$

$\mathcal{G}_0(\mathbf{r}_k,t_l) = \{g_0(\mathbf{r}_i,t_{l+s}|\mathbf{r}_k,t_l) : i = 1, 2, \ldots, n; s = 1, 2, \ldots, m - l + 1\}$ = set of values of the effort-dependent Green function computed from a release of tagged fish in cell $\mathcal{A}_k$ in the interval of time $\mathcal{T}_l$

$\mathcal{G}_0 = \{\mathcal{G}_0(\mathbf{r}_s,t_{l+s-1}) : s = 1, 2, \ldots, n\}$ = set of values of $n$ Green functions from tagged fish releases in cells $\mathcal{A}_s$ correspondingly during the intervals of time $\mathcal{T}_s$ for $s = l, l + 1, \ldots, l + n - 1$

$\mathcal{G}_0^*(\mathcal{T}_j) = \{g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_j) : i, k = 1, 2, \ldots, n\}$ = set of effort-dependent transition probability densities for the interval of time $\mathcal{T}_j$

$\mathcal{G}_0^* = \mathcal{G}_0^*(\mathcal{T}_{l+n}) \cup \mathcal{G}_0^*(\mathcal{T}_{l+n+1}) \cup \ldots \cup \mathcal{G}_0^*(\mathcal{T}_m) = \{g_0(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_j) : i, k = 1, 2, \ldots, n; j = l + n, l + n + 1, \ldots, m\}$ = set of effort-dependent transition probability densities in the intervals of time $\mathcal{T}_j$ for $j = l + n, l + n + 1, \ldots, m$

$\mathcal{G}^* = \{g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_j) : i, k = 1, 2, \ldots, n; j = l + n, l + n + 1, \ldots, m\}$ = set of effort-independent transition probability densities in the intervals of time $\mathcal{T}_j$ for $j = l + n, l + n + 1, \ldots, m$

$\langle f(\mathbf{r}) \rangle (t|\mathbf{r}',t') = \int_{\mathcal{A}} d^2\mathbf{r}\, f(\mathbf{r}) g(\mathbf{r},t|\mathbf{r}',t')$

$\langle f(\mathbf{r}_i) \rangle (t_{j+1}|\mathbf{r}_k,t_j) = \sum_{i=1}^{n} \mathcal{A}_i f(\mathbf{r}_i) g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_j)$

l.h.s., r.h.s. = left-hand side, right-hand side.

## 2. Problem Statement and Formulation

Assume that almost all of a fish population is contained in a domain $\mathcal{A} \in \mathbf{R}^2$. Although in reality, fish populations inhabit three-dimensional space, this work will deal with highly migratory species whose vertical movement is negligible compared with their horizontal motion. Such is the case, for example, of pelagic species of fish.

Assume also that the population is being exploited with effort density $e(\mathbf{r},t)$ over the time interval $\mathcal{T}_l = [t_l,t] = t - t_l$. During that time interval, a catch density rate $c(\mathbf{r},t)$ is realized. Because I wish to determine how an increased fishing effort in a portion of $\mathcal{A}$ will affect the catch density rate in another portion of $\mathcal{A}$, the movement patterns of the population must be determined. To this end, a tagging experiment with distinguishable tags is initiated at time $t_T \in \mathcal{T}_l$ which results in a tagged fish catch density rate $c_T(\mathbf{r},t)$ in the interval of time $\mathcal{T}_T = [t_T,t] \subseteq \mathcal{T}_l$. In addition, I wish to calculate the recruitment density rate $r(\mathbf{r},t)$ and estimate parameters assuming that the fish population is accurately modeled by a diffusive population that drifts.

I have previously considered the fisheries interaction problem formulated above making no use of differential equations by applying the principle of linear superposition (Salvadó 1994). Here, I will go about solving this problem by use of the Green functions associated with population field equations derived from the Rayleigh transport theorem (Okubo 1980). This theorem states that any population that is in motion and distributed in a space–time continuum must satisfy the relationship

$$\text{(1)} \quad \frac{\partial p\,(\mathbf{r},t)}{\partial t} + \nabla\cdot\mathbf{j}(\mathbf{r},t) = s(\mathbf{r},t)$$

where $p$ is the population density, $\mathbf{j}$ is the flux of $p$ (the amount of transport of population across a unit area in unit time), and $s$ is the source (+) or sink (−) rate densities of $p$ at space–time point $(\mathbf{r},t)$. The flux $\mathbf{j}$ will be assumed to be the result of an operation on the spatial distribution of $p$ that results in a differential expression that is linear in $p$.

For a population whose movement and distribution in space–time are structured by age, the transport equation given in (1) must be modified. If $p(\mathbf{r},t,a)$ is the population density of individuals of age $a$ at space–time point $(\mathbf{r},t)$, the transport equation is given by (Murray 1989)

$$\text{(2)} \quad \frac{\partial p(\mathbf{r},t,a)}{\partial t} + \frac{\partial p(\mathbf{r},t,a)}{\partial a} + \nabla\cdot\mathbf{j}\,(\mathbf{r},t,a) = s(\mathbf{r},t,a)\,.$$

However, because aging is at the same rate as the passing of time, transforming (2) with the set of transformations for $t > a$

$$t' = t$$
$$a' = t - a$$
$$\mathbf{r}' = \mathbf{r}$$

leads to the transport equation

$$\text{(3)} \quad \frac{\partial p(\mathbf{r}',t',t'-a')}{\partial t'} + \nabla'\cdot\mathbf{j}(\mathbf{r}',t',t'-a') = s(\mathbf{r}',t',t'-a')\,.$$

Equation (3) is of the same form as (1) except that the latter has fields with two arguments of time. It follows that the solutions of the age-dependent field equations can be inferred from those expressions corresponding to age-independence. Therefore, for simplicity, this exposition will be for the age-independent case.

A population density is said to be conserved if the source and/or sink term $s$ in Eq. (1) vanishes, but in the general treatment here, population density may be nonconservative. With $d(\mathbf{r},t)$ as the natural death density rate, and $r(\mathbf{r},t)$ as the recruitment density rate, $s(\mathbf{r},t)$ is generally given by

$$s(\mathbf{r},t) = r(\mathbf{r},t) - [d(\mathbf{r},t) + c(\mathbf{r},t)]\,.$$

The biomass volume of fish populations is small in comparison with the volume of water they inhabit and, therefore, I shall assume that the population is dilute. As a consequence of this assumption, I can make some linear approximations. Because the catch density rate must be a function of population density (i.e., there can be no catch if there are no fish), expanding $c(p)$ in a Taylor series about $p = 0$ up to the linear term yields $c(p) = fp$ ($c(0) = 0$ necessarily), where $f = [\partial c(p)/\partial p]_{p=0}$ is the death rate due to fishing. Because $f$ must be a function of effort density (i.e., there can be no fishing death if there is no fishing), expanding $f(e)$ in a Taylor series about $e = 0$ up to the linear term yields $f(e) = qe$ ($f(0) = 0$ necessarily), where $q = [\partial^2 c(p,e)/\partial p \partial e]_{p=e=0}$ is the catchability. Therefore, for low population and effort densities, one can assume the model for catch density rate to be

$$\text{(4)} \quad c(\mathbf{r},t) = f(\mathbf{r},t)\,p(\mathbf{r},t) = q(\mathbf{r},t)\,e(\mathbf{r},t)\,p(\mathbf{r},t)\,.$$

Similarly, the natural death density rate $d$ must be a function of population density. Therefore, with $m$ the natural death rate (i.e., natural mortality) and $d(p)$ expanded in a Taylor series about $p = 0$ up to the linear term (where $d(0) = 0$ necessarily), at low population density the model for natural death density rate can be assumed to be

$$(5)\quad d(\mathbf{r},t) = m(\mathbf{r},t)\,p(\mathbf{r},t)\,.$$

In the method of analyzing the dynamics of populations in space–time that follows, it is not necessary to invoke a particular model for the source term corresponding to recruitment density rate. However, as I shall show, it is possible to determine empirically the recruitment density rate once the population density due to recruitment is calculated.

I shall further assume that the population drifts with velocity $\mathbf{v}(\mathbf{r},t)$. The population is also assumed to disperse diffusively with diffusivity $k(\mathbf{r},t)$. Then, consistent with the assumption of linearity due to diluteness used in the formulation of the catch density rate and natural death density rate, the flux of the population density is

$$(6)\quad \mathbf{j}(\mathbf{r},t) = \left[\mathbf{v}(\mathbf{r},t) - k(\mathbf{r},t)\nabla\right]p(\mathbf{r},t)\,.$$

Therefore, the field equation the population density is assumed to satisfy is

$$(7)\quad \left[\frac{\partial}{\partial t} + \mathcal{L}_0\right]p(\mathbf{r},t) = r(\mathbf{r},t)$$

in the spatial domain $\mathbf{r} \in \mathcal{A}$, where $\mathcal{L}_0$ is a differential operator that operates only on the spatial distribution of $p(\mathbf{r},t)$ and is given by

$$(8)\quad \mathcal{L}_0 = b_0(\mathbf{r},t) + \mathbf{b}_1(\mathbf{r},t)\cdot\nabla + b_2(\mathbf{r},t)\,\Delta$$

where

$$\nabla = \mathbf{i}\frac{\partial}{\partial x} + \mathbf{j}\frac{\partial}{\partial y}$$

$$\Delta = \nabla\cdot\nabla = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$$

$$(9)\quad b_0(\mathbf{r},t) = z(\mathbf{r},t) + \nabla\cdot\mathbf{v}(\mathbf{r},t)$$

$$b_1(\mathbf{r},t) = \mathbf{v}(\mathbf{r},t) - \nabla\,k(\mathbf{r},t)$$

$$b_2(\mathbf{r},t) = -k(\mathbf{r},t)$$

and $z(\mathbf{r},t) = m(\mathbf{r},t) + f(\mathbf{r},t)$. The restrictions on the parameters of the field equation are that $\int_{t_T}^{t} d\tau z(\mathbf{r},\tau) \ge 0$, $\int_{t_T}^{t} d\tau k(\mathbf{r},\tau) \ge 0$, and that $\nabla\cdot\mathbf{v}(\mathbf{r},t)$ and $\Delta k(\mathbf{r},t)$ exist. For $b_0(\mathbf{r},t) = r(\mathbf{r},t) = 0$, field equation (7) is a Fokker–Planck equation used in the study of stochastic processes where probability is conserved (Gardiner 1990). In the general treatment of this work, $b_0(\mathbf{r},t) \neq 0$ and $r(\mathbf{r},t) \neq 0$. Because these terms represent sources and/or sinks of population, probability will not be conserved.

The domain of the population is finite, so I must discuss the boundary $\partial\mathcal{A}$ of $\mathcal{A}$. For the purposes of this paper the boundary $\partial\mathcal{A}$ is defined as the line at the edge of $\mathcal{A}$ (i.e., $\partial\mathcal{A} \subset \mathcal{A}$) beyond which the population is unlikely to inhabit due to unfavorable physicobiological conditions. In general, fish populations have two types of boundaries: well-defined ones delineating, for example, the water–land interface and fuzzy ones demarcating, for example, lines beyond which if a member of the population strays is likely to perish due to unfavorable environmental conditions. It can be shown (Appendix A) that with a prescribed population density at an initial time (initial condition) the solution of (7) is unique and "simply" represented when $p(\mathbf{r},t)$ or the component normal to $\partial\mathcal{A}$ of $\nabla p(\mathbf{r},t)$ vanish on $\partial\mathcal{A}$. By "simple" representation of the solution, I mean that the Green function associated with (7) is a simple function of measurable quantities, a concept that will become evident when I discuss the solutions. However, the required simplicity does lead to physicobiological pertinent boundaries of fish population domains.

Consider the first boundary condition

$$(10)\quad p(\mathbf{r},t) = 0$$

for $\mathbf{r} \in \partial\mathcal{A}$. The drift $\mathbf{v}(\mathbf{r},t)$ could be the motion of the medium, relative to a fixed coordinate system, that the population is riding or fighting. The diffusivity $k(\mathbf{r},t)$ is ultimately an environmental variable that could be negatively correlated with the amount of food encountered by the population at space–time point $(\mathbf{r},t)$. Low food availability in a region of the population domain would mean that the random motion of a foraging fish population in that region could increase and, according to (7), would be "pushed" in the opposite direction in which $k(\mathbf{r},t)$ changes the fastest towards a region of lower $k$. As I shall later show in an example, an increased diffusivity at a particular space–time point results in a decrease of the population density at that point. Although the natural death rate $m(\mathbf{r},t)$ has limits imposed by evolution, it is dependent also on environmental factors such as food availability and probability of encounters with predators. A high value for $m(\mathbf{r},t)$ could mean low food availability and/or high probability of encounter with a predator at space–time point $(\mathbf{r},t)$. Therefore, the boundary condition (10) would be a good model of a "fuzzy" population boundary preceded by regions of increasing diffusivity and/or natural death rate. A boundary on which (10) holds is aptly known as the perfectly absorbing boundary (Okubo 1980; Gardiner 1990). In the mathematical literature, this boundary condition is known as homogeneous Dirichlet conditions.

A second boundary condition mentioned above that leads to unique simple solutions of (7) (together with an initial condition) is formulated by considering the integral over $\mathcal{A}$ of equation (1) and applying the Divergence Theorem (Courant and Hilbert 1953) to the term containing the divergence of $\mathbf{j}(\mathbf{r},t)$. Letting $\mathbf{n}_\perp$ be the unit vector normal to $\partial\mathcal{A}$ pointing outward, then

$$\int_{\mathcal{A}} d^2\mathbf{r}\,\frac{\partial p(\mathbf{r},t)}{\partial t} = \int_{\mathcal{A}} d^2\mathbf{r}\,s(\mathbf{r},t) - \oint_{\partial\mathcal{A}} dl\,\mathbf{n}_\perp\cdot\mathbf{j}(\mathbf{r},t)\,.$$

This states that the change in population density over time is due to the sinks and sources of population in $\mathcal{A}$ and the flux of $p(\mathbf{r},t)$ across $\partial\mathcal{A}$. However, because $\mathcal{A}$ is the domain of the population, the flux of $p$ across $\partial\mathcal{A}$ must vanish and the change in population density is due to the sources and sinks. Therefore,

$$\mathbf{n}_\perp\cdot\mathbf{j}(\mathbf{r},t) = 0$$

for $\mathbf{r} \in \partial\mathcal{A}$. Using (6), it can be written as

$$\mathbf{n}_\perp \cdot \nabla p(\mathbf{r},t) = \frac{\mathbf{n}_\perp \cdot \mathbf{v}(\mathbf{r},t)}{k(\mathbf{r},t)}\, p(\mathbf{r},t)$$

in the domain $\mathbf{r} \in \partial\mathcal{A}$. Furthermore, because $\mathcal{A}$ is the domain of the population the vanishing of the flux must be due to the inability of any member of the population to cross $\partial\mathcal{A}$. Therefore, the component of the drift velocity normal to $\partial\mathcal{A}$ must also vanish (i.e., $\mathbf{n}_\perp \cdot \mathbf{v}(\mathbf{r},t) = 0$ for $\mathbf{r} \in \partial\mathcal{A}$) and the boundary condition reduces to

$$(11) \quad \mathbf{n}_\perp \cdot \nabla p(\mathbf{r},t) = 0$$

for $\mathbf{r} \in \partial\mathcal{A}$. A boundary on which (11) holds is aptly known as the perfectly reflecting boundary (Okubo 1980; Gardiner 1990). In the mathematical literature, this boundary condition is known as homogeneous Neumann conditions. This boundary condition is appropriate for the ocean–land boundary.

I shall assume throughout this work that the boundary of the domain of the population is composed of segments or portions which are perfectly absorbing and the remainder perfectly reflecting. If $\partial\mathcal{A}_A$ is the total of the absorbing segments, and $\partial\mathcal{A}_R$ is the total of the reflecting segments, then $\partial\mathcal{A} = \partial\mathcal{A}_A + \partial\mathcal{A}_R$. The solution of the field equation (7), with a prescribed initial condition, satisfying the mixed boundary conditions is unique (Appendix A).

Using this formulation, I shall show that data from a tagging experiment properly performed may be used to construct an approximate representation of a Green function. I shall, therefore, develop an empirical technique to construct Green functions using tagged fish catch and effort data and use these results for a fishery interaction problem and the calculation of model parameters.

## 3. Problem Solution

In this section, I will develop the Green function as an approximate representation of a tagging experiment, list its properties, and use it to represent the tagged and untagged fish population densities. For an intuitive approach to the developments in this section which makes no use of differential equations, see Salvadó (1994).

### 3.1. Effort-Dependent Green Function

In this subsection, I formulate and find representations of the solutions for the tagged and untagged portion of the population in terms of a point-source solution that is dependent on the death rate due to fishing. I shall also show how the point-source solutions are constructed from the fields $c_T$ and $e$. Although these are correct solutions to model the population field at one level of fishing effort, unless $m(\mathbf{r},t) \gg f(\mathbf{r},t)$, they are not of much use for the case of considering the interaction between different cells (for the time being defined as a small subset of $\mathcal{A}$) of the domain of the population at various levels of effort.

#### *3.1.1. Tagged fish dynamics*

Consider a tagging experiment in which $N_T$ tagged fish are released in an area small compared with $\mathcal{A}$ about position $\mathbf{r}_T$ beginning at time $t_T \in \mathcal{T}_I$. The duration of the tagged fish release is short conpared with $\mathcal{T}_T$, where $t \gg t_T$. I shall index the number of tagged fish, location, and initial time of release by writing $N_T(\mathbf{r}_T,t_T)$.

Let $\mathcal{L}_0$ be a linear differential operator which contains the terms of the field equation that describe the natural and fishing death rates and the spatial dynamics. Consistent with (7) and the general fish population problem formulated in Section 2, the tagged fish population density $p_T(\mathbf{r},t)$ must satisfy a field equation of the form

$$(12) \quad \left[\frac{\partial}{\partial t} + \mathcal{L}_0\right] p_T(\mathbf{r},t) = 0$$

in the space–time domain $\mathbf{r} \in \mathcal{A}$, $t \geq t_T$.

The initial condition of the tagged fish release process will be approximated as if the release is at one point (i.e., at $\mathbf{r} = \mathbf{r}_T$) and instantaneous (i.e., at $t = t_T$): an approximate representation of the initial condition of the population density of tagged fish is

$$(13) \quad p_T(\mathbf{r},t_T) = N_T(\mathbf{r},t_T)\, \delta(\mathbf{r} - \mathbf{r}_T)$$

in the space domain $\mathbf{r} \in \mathcal{A}$ and where $\delta$ is a two-dimensional Dirac delta function (Lighthill 1964; Butkov 1968). The discretization of space–time will relax the condition of an instantaneous release at a point of all the tagged fish.

The boundary $\partial\mathcal{A} = \partial\mathcal{A}_A + \partial\mathcal{A}_R$ is assumed composed of segments on which it is absorbing ($\partial\mathcal{A}_A$) and those on which it is reflecting ($\partial\mathcal{A}_R$). Therefore, $p_T(\mathbf{r},t)$ satisfies

$$(14) \quad p_T(\mathbf{r},t) = 0$$

on the space–time domain $\mathbf{r} \in \partial\mathcal{A}_A$, $t \geq t_T$, and

$$(15) \quad \mathbf{n}_\perp \cdot \nabla p_T(\mathbf{r},t) = 0$$

in the space–time domain $\mathbf{r} \in \partial\mathcal{A}_R$, $t \geq t_T$.

I seek the solution of (12) that satisfies conditions (13), (14), and (15). To this end, I consider the Green function that is associated with (12) for a source space–time point at $(\mathbf{r}',t')$. With respect to the receiver space–time coordinates $(\mathbf{r},t)$, the Green function associated with (12) satisfies (Appendix A)

$$(16) \quad \left[\frac{\partial}{\partial t} + \mathcal{L}_0\right] g_0(\mathbf{r},t|\mathbf{r}',t') = \delta(\mathbf{r} - \mathbf{r}')\, \delta(t - t')$$

in the domain $\mathbf{r} \in \mathcal{A}$, a causality condition

$$(17) \quad g_0(\mathbf{r},t|\mathbf{r}',t') = 0 \text{ if } t < t'$$

in the domain $\mathbf{r} \in \mathcal{A}$, and boundary conditions

$$g_0(\mathbf{r},t|\mathbf{r}',t') = 0$$

for $\mathbf{r} \in \partial\mathcal{A}_A$ and

$$\mathbf{n}_\perp \cdot \nabla g_0(\mathbf{r},t|\mathbf{r}',t') = 0$$

for $\mathbf{r} \in \partial\mathcal{A}_R$.

The solution that satisfies (12), (13), (14), and (15) is given by (Appendix A)

$$(18) \quad p_T(\mathbf{r},t) = g_0(\mathbf{r},t|\mathbf{r}_T,t_T)\, N_T(\mathbf{r}_T,t_T)\,.$$

As an example, if $\mathcal{L}_0$ is given by

$$(19)\quad \mathcal{L}_0 = z(t) + \mathbf{v}(t)\cdot\nabla - k(t)\,\Delta\,,$$

then the solution of (16) in an unbounded domain that satisfies the causality condition (17) and boundary condition

$$\lim_{r\to\infty} g_0(\mathbf{r},t|\mathbf{r}',t') = 0$$

where $r = \sqrt{\mathbf{r}\cdot\mathbf{r}}$ for a source at $(\mathbf{r}_T,t_T)$ is

$$(20)\quad g_0(\mathbf{r},t|\mathbf{r}_T,t_T) = \exp\left[-\int_{\mathcal{T}_T} d\tau z(\tau)\right]$$

$$\times\, \mathcal{N}\left(\mathbf{r}_T + \int_{\mathcal{T}_T} d\tau\mathbf{v}(\tau),\sigma^2\right) h(t-t_T)\,,$$

$\mathcal{N}(\mathbf{r}_T,\sigma^2)$ is the normal distribution centered at $\mathbf{r}_T$ with variance $\sigma^2$ given by

$$(21)\quad \sigma^2(t,t_T) = 2\int_{\mathcal{T}_T} d\tau k(\tau)\,,$$

and $h(t-t_T)$ is the Heaviside step function defined as

$$h(t-t_T) = \begin{cases} 0 \text{ if } t < t_T \\ 1 \text{ if } t \geq t_T\,. \end{cases}$$

As can be appreciated the amplitude of (20) decreases when $m$ and/or $k$ increase. It is initially (i.e., at $t = t_T$) a normal distribution centered at $\mathbf{r} = \mathbf{r}_T$ with vanishing variance (i.e., a Dirac delta function). For $t < t_T$ the distribution vanishes, while for $t > t_T$ the distribution spreads at a rate that depends on the diffusion coefficient $k$, and the mean drifts at a rate determined by the drift velocity $\mathbf{v}$. While the distribution $\mathcal{N}$ is normalized for all $t \geq t_T$, the distribution $g_0$ does not conserve probability. Because $z(t) = m(t) + f(t) > 0$, the exponential function or survivability coefficient (Ricker 1975) leading $\mathcal{N}$ in (20) decreases with increasing time from an initial value of unity. I shall show that these properties of $g_0$ are general properties of the point-source solutions associated with (19). To see this, I solve for $g_0$ from (18). With the use of (4), I can express $g_0$ as a function of the measured fields $e$ and $c_T$ as

$$(22)\quad g_0(\mathbf{r},t|\mathbf{r}_T,t_T) = \frac{p_T(\mathbf{r},t)}{N_T(\mathbf{r}_T,t_T)} = \frac{c_T(\mathbf{r},t)}{q(\mathbf{r},t)\,e(\mathbf{r},t)\,N_T(\mathbf{r}_T,t_T)}\,.$$

Because I know the number $N_T$ of tagged fish released at space–time point $(\mathbf{r}_T,t_T)$, and I have $c_T(\mathbf{r},t)$ and $e(\mathbf{r},t)$ in the interval of time $\mathcal{T}_T$, I can construct empirically the Green function $g_0(\mathbf{r},t|\mathbf{r}_T,t_T)$ in the interval of time $\mathcal{T}_T$ if I have $q(\mathbf{r},t)$.

The Green function $g_0$ has a series of properties that can be inferred. The first of these properties will allow the estimation of $q(\mathbf{r},t)$ as follows.

*A. Initial* — Assuming tagged fish disperse at a finite rate, initially they must be present at the point of release only. Therefore, for a source space-time point at $(\mathbf{r}_T,t_T)$, $g_0$ must satisfy

$$g_0(\mathbf{r},t_T|\mathbf{r}_T,t_T) = \delta(\mathbf{r}-\mathbf{r}_T)\,.$$

Analytically this can be deduced by dividing through (13) by the number of tagged fish released. Therefore, multiplying expression (22) by $q(\mathbf{r},t)$ and integrating over the spatial domain and application of the initial property of $g_0$ for $t \to t_T$ yields

$$(23)\quad q(\mathbf{r}_T,t_T) = \frac{1}{N_T(\mathbf{r}_T,t_T)}\int_{\mathcal{A}} d^2\mathbf{r}\,\frac{c_T(\mathbf{r},t_T)}{e(\mathbf{r},t_T)}\,.$$

Dimensional analysis of (23) reveals that $q$ has the dimensions of area × time$^{-1}$. The dependence of its value on spatiotemporal location will ultimately dictate in how many cells and intervals of time must tagged fish be released in order to characterize the pattern of fish movement within $\mathcal{A}$. The empirical construction of $g_0(\mathbf{r},t_T|r',t')$ requires knowledge of $q(\mathbf{r},t)$ for all $\mathbf{r} \in \mathcal{A}$ and all $t \in \mathcal{T}_T$. The calculation of $q$ by (23) requires that it be done at the space–time point of the tagged fish release. It follows, therefore, that to construct $q(\mathbf{r},t)$ for all $\mathbf{r} \in \mathcal{A}$ and all $t \in \mathcal{T}_T$ in principle requires performing nondenumerably infinite tagging experiments if $q$ depends strongly on $(\mathbf{r},t)$. However, as will be discussed later, discretization and weak dependence of $q$ on $(\mathbf{r},t)$ will allow some approximations.

The accurate estimation of $q$ using (23) requires that the loss of tagged fish due to natural mortality during the time of release be negligible. It is, therefore, important to release the tagged fish in as short a time as possible. If $[t_T, t_{T+\delta}]$ is the interval of time over which the tagged fish are released, the required condition of small loss of tagged fish due to natural death rate during the time of release will be fullfilled if $m(\mathbf{r},t_T) \ll 1/[t_T,t_{T+\delta}]$. Other properties of $g_0$ are as follows.

*B. Dimensional* — Dimensional analysis of (22) reveals that $g_0$ is a density. That is, $g_0$ has the dimensions of area$^{-1}$.

*C. Causal* — Because tagged fish can exist in their domain only if they are present at an equal or earlier time, for a source time $t_T$, $g_0$ must satisfy

$$g_0(\mathbf{r},t|\mathbf{r}_T,t_T) = 0 \text{ for } t < t_T\,.$$

*D. Normalization* — As a consequence of the initial property,

$$\int_{\mathcal{A}} d^2\mathbf{r}\,g_0(\mathbf{r},t_T|\mathbf{r}_T,t_T) = 1\,.$$

*E. Probabilistic* — Because the number of tagged fish recaptured cannot be greater than those released, for $t \geq t_T$,

$$0 \leq g_0(\mathbf{r},t|\mathbf{r}_T,t_T) \leq \delta(\mathbf{r}-\mathbf{r}_T)$$

and therefore,

$$0 \leq \int_{\mathcal{A}} d^2\mathbf{r}\,g_0(\mathbf{r},t|\mathbf{r}_T,t_T) \leq 1\,.$$

Hence, $g_0\,(\mathbf{r},t|\mathbf{r}_T,t_T)$ can be regarded as the probability density of a tagged fish surviving the movement to position $\mathbf{r}$ from $\mathbf{r}_T$ during the interval of time $\mathcal{T}_T$ when fishing takes place in that interval of time. Assuming that the recaptured tagged fish are not rereleased, I will call $g_0$ the effort-dependent Green function.

*F. Nonconservation of probability* — Because tagged fish are being removed from their domain by natural and fishing deaths, in general it must be true that for $t > t_T$,

$$\int_{\mathcal{A}} d^2\mathbf{r}\, g_0(\mathbf{r},t|\mathbf{r}_T,t_T) < 1 \, .$$

In order to derive the property of linear superposition of Green functions, consider the solution (18) which I will write as

$$(24) \quad p_T(\mathbf{r}',t') = g_0(\mathbf{r}',t'|\mathbf{r}_T,t_T)\, N_T(\mathbf{r}_T,t_T) \, .$$

Suppose I wanted to use the final condition $p_T(\mathbf{r}',t')$ of (24) as the initial condition of a tagged population problem. The population density must then satisfy field equation (12) and initial condition

$$p_T(\mathbf{r}',t') = \frac{c_T(\mathbf{r}',t')}{q(\mathbf{r}',t')\, e(\mathbf{r}',t')}$$

for $\mathbf{r}' \in \mathcal{A}$ (or some other estimate at $(\mathbf{r}',t')$ of $p_T$) and boundary conditions (14) and (15). The solution is given by (Appendix A)

$$(25) \quad p_T(\mathbf{r},t) = \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t')\, p_T(\mathbf{r}',t') \, .$$

Dividing (25) by $N_T(\mathbf{r}_T,t_T)$ and using the definition of $g_0$ given by (22) leads to the following property.

*G. Linear superposition of probability densities* — The probability density satisfies

$$(26) \quad g_0(\mathbf{r},t|\mathbf{r}_T,t_T) = \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t')\, g_0(\mathbf{r}',t'|\mathbf{r}_T,t_T) \, .$$

Another important property of $g_0$ is its periodicity.

*H. Periodicity* — A Green function is said to be periodic in time, of period $\mathcal{T}$, if $\mathcal{T}$ is a constant such that

$$g(\mathbf{r},t|\mathbf{r}',t') = g(\mathbf{r},t+\mathcal{T}|\mathbf{r}',t'+\mathcal{T})$$

(Tolstov 1962). A spatial periodicity can also be defined.

### *3.1.2. Untagged fish dynamics*

Consistent with (7) and the general fishery problem formulated in the foregoing section, I would like to find expressions for the population density of the untagged portion in the interval of time $\mathcal{T}_I$. However, because the empirical Green function is constructed for $t \geq t_T \geq t_I$, in general it is not possible to define empirically the population density in the interval of time $t_I \leq t \leq t_T$ from a tagging campaign initiated at time $t_T$. Therefore, I shall pose the problem for the untagged portion of the population in the interval of time $\mathcal{T}_T$.

The population density of untagged fish $p(\mathbf{r},t)$ obeys the field equation

$$(27) \quad \left[\frac{\partial}{\partial t} + \mathcal{L}_0\right] p(\mathbf{r},t) = r(\mathbf{r},t)$$

in the space–time domain $\mathbf{r} \in \mathcal{A}$, $t \geq t_T$ subject to initial condition

$$(28) \quad p(\mathbf{r},t_T) = p_{\text{in}}(\mathbf{r}) = \frac{c(\mathbf{r},t_T)}{q(\mathbf{r},t_T)\, e(\mathbf{r},t_T)}$$

in the domain $\mathbf{r} \in \mathcal{A}$ (or some other estimate at $(\mathbf{r},t_T)$ of $p$) and boundary conditions

$$(29) \quad p(\mathbf{r},t) = 0$$

in the domain $\mathbf{r} \in \partial\mathcal{A}_A$, $t \geq t_T$ and

$$(30) \quad \mathbf{n}_\perp \cdot \nabla p(\mathbf{r},t) = 0$$

in the domain $\mathbf{r} \in \partial\mathcal{A}_R$, $t \geq t_T$.

Because the differential operators for the tagged and untagged portions of the fish population are identical, even though their inhomogeneous term and initial conditions differ, this means that the movement and survivability of tagged and untagged fish are linked through the equality of their Green functions. In practice, this is true only if sufficient numbers of tagged fish are released so that $g_0$ constructed as indicated by (22) approximately represents the average movement and survivability of the total fish population.

The solution that satisfies (27), (28), (29), and (30) is (Appendix A)

$$(31) \quad p(\mathbf{r},t) = \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t_T)\, p_{\text{in}}(\mathbf{r}') + u_0(\mathbf{r},t)$$

where the field $u_0(\mathbf{r},t)$ is the contribution to the population density due to recruitment and is given by

$$(32) \quad u_0(\mathbf{r},t) = \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t')\, r(\mathbf{r}',t') \, .$$

Multiplying (31) by the fishing death rate $f(\mathbf{r},t)$ yields the expression for the catch density rate:

$$(33) \quad c(\mathbf{r},t) = f(\mathbf{r},t)\left[\int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t_T)\, p_{\text{in}}(\mathbf{r}') + u_0(\mathbf{r},t)\right]$$

The contribution to the population density due to recruitment at the level of exploitation at which the empirical probability density $g_0$ was constructed can be computed by use of (33). Solving for $u_0$, I have

$$(34) \quad u_0(\mathbf{r},t) = \frac{c(\mathbf{r},t)}{f(\mathbf{r},t)} - \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t_T)\, p_{\text{in}}(\mathbf{r}') \, .$$

Because in the interval of time $\mathcal{T}_T$, I know $f(\mathbf{r},t)$ and the resulting $c(\mathbf{r},t)$, (34) can be used to calculate $u_0(\mathbf{r},t)$ at the level of effort for which $g_0(\mathbf{r},t|\mathbf{r}',t_T)$ was constructed. However, in general, I cannot use equation (33) to compute the catch density rate at a new level of effort unless I perform another tagging experiment at the desired level. The survivability embedded in $g_0$ depends on the level of exploitation during the recapture of the tagged fish. Therefore, although these equations using $g_0$ are valid for modeling the movement and distribution of a fish population, they are in general useful only at the level of effort for which $g_0$ was constructed. In general, no other case can be rigourously considered. In Section 4, I shall show that if the natural death rate is much greater than that due to fishing, the equations derived in this section can be used for a fisheries interaction study. However, in order to be able to consider the general fisheries interaction problem formulated in Section 2 without having to perform tagging experiments for all the levels of effort that wish to be considered. I need to reformulate the problem so that the solutions for the population density are in terms of a Green function that is effort independent.

## 3.2. Effort-Independent Green Function

In this subsection, I shall find the solutions for the population density for tagged and untagged fish in terms of a Green function that is effort independent. I shall also show how to construct the effort-independent Green function from knowledge of the effort-dependent one. This new Green function satisfies, other than the fact that it is independent of fishing death rate, properties identical to those of $g_0$.

### *3.2.1. Tagged fish dynamics*

Consider again a tagging experiment in which $N_T$ tagged fish are released in an area small compared with $\mathcal{A}$ about position $\mathbf{r}_T$ beginning at time $t_T \in \mathcal{T}_I$ with a duration short compared with $\mathcal{T}_T$ where $t \gg t_T$. Here again, I shall index the number of tagged fish, location, and initial time of release by writing $N_T(\mathbf{r}_T,t_T)$. However, in this case, I shall pose the problem with a differential operator that is independent of the fishing death rate, and I shall pass on to the inhomogeneous part of the field equation the responsibility for embedding into the solution for the population density the information of catch density rate.

Let $\mathcal{L}$ be a linear differential operator which contains the terms of (7) that describe the natural death rate and the spatial dynamics. In terms of operator $\mathcal{L}_0$, operator $\mathcal{L}$ is given by

$$\mathcal{L} = \mathcal{L}_0 - f(\mathbf{r},t) .$$

Consistent with (7) and the general fishery problem formulated in Section 2, the tagged fish population density must therefore satisfy a field equation of the form

$$(35)\quad \left[\frac{\partial}{\partial t} + \mathcal{L}\right] p_T(\mathbf{r},t) = -c_T(\mathbf{r},t)$$

in the space–time domain $\mathbf{r} \in \mathcal{A}$, $t \geq t_T$, subject to initial condition (13) and boundary conditions (14) and (15). The tagged fish catch density rate is now the inhomogeneous term of the field equation. It is a negative contribution because it is a sink of population. The solution that satisfies (35), (13), (14), and (15) is given by (Appendix A)

$$(36)\quad p_T(\mathbf{r},t) = g(\mathbf{r},t|\mathbf{r}_T,t_T)\, N_T(\mathbf{r}_T,t_T) - \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g(\mathbf{r},t|\mathbf{r}',t')\, c_T(\mathbf{r}',t') .$$

I need to determine how the effort-independent Green function is related to $g_0$. On dividing equation (36) by $N_T$ and using the definition of $g_0$ given by (22), the relation between the effort-dependent and effort-independent Green functions becomes

$$(37)\quad g(\mathbf{r},t\,|\mathbf{r}_T,t_T) = g_0(\mathbf{r},t|\mathbf{r}_T,t_T) + \frac{1}{N_T(\mathbf{r}_T,t_T)} \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g(\mathbf{r},t|\mathbf{r}',t')\, c_T(\mathbf{r}',t')$$

which is an integral equation where $g(\mathbf{r},t|\mathbf{r}',t')$ is the unknown. The exact solution to integral equation (37) is given by the Neumann series (Courant and Hilbert 1953; Byron and Fuller 1970)

$$(38)\quad g(\mathbf{r},t|\mathbf{r}_T,t_T) = \sum_{i=0}^{\infty} g_i(\mathbf{r},t|\mathbf{r}_T,t_T)$$

where

$$(39)\quad g_i(\mathbf{r},t|\mathbf{r}_T,t_T) = \frac{1}{N_T(\mathbf{r}_T,t_T)} \int_{\mathcal{T}_T} dt' \times \int_{\mathcal{A}} d^2\mathbf{r}'\, g_{i-1}(\mathbf{r},t|\mathbf{r}',t')\, c_T(\mathbf{r}',t')$$

for $i = 1, 2, \ldots$. The series (38) converges over an arbitrary interval of time whenever the number of tagged fish recaptured is less than the total number of tagged fish available at the beginning of the interval (Appendix B), and therefore, it converges uniformly to the solution under that condition (Byron and Fuller 1970).

To discuss some approximations, consider the total number of tagged fish recaptured in the interval of time $\mathcal{T}_T$:

$$N_R(t) = \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, c_T(\mathbf{r}',t') .$$

If $N_R < N_T$ but $N_R \nless N_T$, the approximation

$$g(\mathbf{r},t|\mathbf{r}_T,t_T) \approx g_0(\mathbf{r},t|\mathbf{r}_T,t_T) + g_1(\mathbf{r},t|\mathbf{r}_T,t_T)$$
$$\approx g_0(\mathbf{r},t|\mathbf{r}_T,t_T) + \frac{1}{N_T(\mathbf{r}_T,t_T)} \int_{\mathcal{T}_T} dt' \times \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t')\, c_T(\mathbf{r}',t')$$

can be used. However, if $N_R \ll N_T$, which implies $m(\mathbf{r},t) \gg f(\mathbf{r},t)$, then the approximation

$$g(\mathbf{r},t|\mathbf{r}_T,t_T) \approx g_0(\mathbf{r},t|\mathbf{r}_T,t_T)$$

is adequate. In a practical computational sense, the expansion is stopped at the term whose contribution is negligible.

The properties of $g$ can be determined with the help of (37). It satisfies all the properties of $g_0$ listed in Subsection (3.1.1.). However, because $g$ does not have fishing death rate included, the survivability associated with it must be in general of larger magnitude than that of $g_0$ except initially. It therefore satisfies

$$g(\mathbf{r},t|\mathbf{r}_T,t_T) \geq g_0(\mathbf{r},t|\mathbf{r}_T,t_T)$$

where the equality holds for $t = t_T$. Therefore, $g(\mathbf{r},t|\mathbf{r}_T,t_T)$ can be regarded as the probability density of a tagged fish surviving the movement to position $\mathbf{r}$ from $\mathbf{r}_T$ during the interval of time $\mathcal{T}_T$ in the absence of fishing during that interval of time. I will therefore call $g$ the effort-independent Green function.

On multiplying (36) by the fishing death rate, the tagged fish catch density rate is the solution of integral equation

$$c_T(\mathbf{r},t) = f(\mathbf{r},t)\left[g(\mathbf{r},t|\mathbf{r}_T,t_T)\, N_T(\mathbf{r}_T, t_T) - \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2r'\, g(\mathbf{r},t|\mathbf{r}',t')\, c_T(\mathbf{r}',t')\right].$$

### 3.2.2. *Untagged fish dynamics*

Consistent with (7), the general fishery problem formulated in Section (2) and the fact that the empirical Green function is known only for $t \geq t_T$, the population density of untagged fish must obey a field equation

$$(40) \quad \left[\frac{\partial}{\partial t} + \mathcal{L}\right] p(\mathbf{r},t) = -c(\mathbf{r},t) + r(\mathbf{r},t)$$

in the space–time domain $\mathbf{r} \in \mathcal{A}$, $t \geq t_T$,, and the conditions (28), (29), and (30). The solution is

$$(41) \quad p(\mathbf{r},t) = \int_{\mathcal{A}} d^2\mathbf{r}' g(\mathbf{r},t|\mathbf{r}',t_I)\, p_{\text{in}}(\mathbf{r}') + u(\mathbf{r},t)$$

$$- \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}' g(\mathbf{r},t|\mathbf{r}',t')\, c(\mathbf{r}',t')$$

where

$$(42) \quad u(\mathbf{r},t) = \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}' g(\mathbf{r},t|\mathbf{r}',t')\, r(\mathbf{r}',t')$$

represents the contribution to the population density attributable to recruitment.

The untagged fish catch density rate is the solution of

$$(43) \quad c(\mathbf{r},t) = f(\mathbf{r},t)\left[\int_{\mathcal{A}} d^2\mathbf{r}' g(\mathbf{r},t|\mathbf{r}',t_T)\, p_{\text{in}}(\mathbf{r}') + u(\mathbf{r},t)\right]$$

$$-f(\mathbf{r},t) \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}' g(\mathbf{r},t|\mathbf{r}',t')\, c(\mathbf{r}',t')\,.$$

Because the catch density rate is known for the level of effort employed during the time interval $\mathcal{T}_T$, then (43) can be applied to those data to determine empirically the field $u$ using

$$(44) \quad u(\mathbf{r},t) = \frac{c(\mathbf{r},t)}{f(\mathbf{r},t)} - \int_{\mathcal{A}} d^2\mathbf{r}' g(\mathbf{r},t|\mathbf{r}',t_T)\, p_{\text{in}}(\mathbf{r}')$$

$$+ \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}' g(\mathbf{r},t|\mathbf{r}',t')\, c(\mathbf{r}',t')\,.$$

Assuming that the recruitment does not change significantly at other levels of effort, catch density rate $c$ can then be computed for differing effort densities $e$ because (43) is valid for any level of effort as opposed to equation (33), which applies only to the measure of effort for which the effort-dependent Green function was constructed.

## 4. Example: Skipjack Tuna Fishery in the Eastern Tropical Atlantic

The following example shows how a subset of the type of fishery models considered in Section 3 can be reduced to a simple calculation whenever the effort density is sufficiently low. The fishery of interest is the skipjack tuna (*Katsuwonus pelamis*) fishery in the five cells of the eastern tropical Atlantic (ETA) indicated in Fig. 1. As a politically interesting question, A. Fonteneau (C.R.O.D.T., B.P. 2241, Dakar, Senegal) asks in a personal communication what effect the doubling of effort in one cell might have on the catches from the other four.

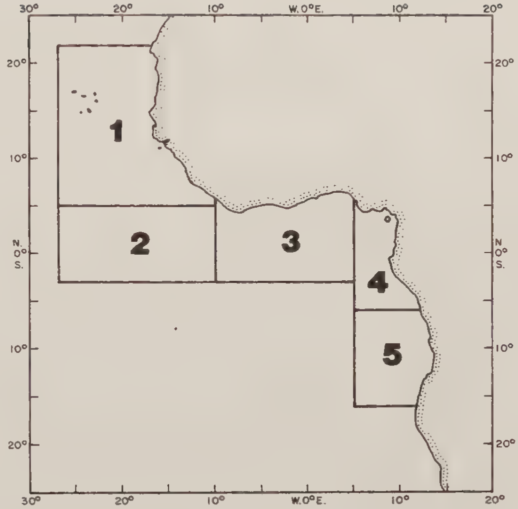

FIG. 1. Eastern tropical Atlantic (ETA) geographic cells: 1, Senegal; 2, Liberia; 3, Ghana; 4, Cape Lopez; 5, Angola.

The data required for the analysis consist solely of the mark and recapture measures from the International Skipjack Year Program, conducted over a 3-yr period by the International Commission for the Conservation of Atlantic Tunas (Symons et al. 1986). Although the corresponding catch and effort densities are also given in Symons et al. (1986), the only information needed here is the reported 5% tag return, together with the assumptions that almost all of the tagged fish survived the trauma of tagging and that almost all of the recaptured tags were reported. As I will show, the fishing effort expended during the experiment was sufficiently low to permit me to regard the dynamic catch density rate as approximately a linear function of effort density.

In the most extreme case, all of the $N_R = 5 \times 10^{-2} N_T$ recovered tags could have been taken in just one of the five cells over a single time interval corresponding to the space–time point $(\mathbf{r}_R, t_R)$ for $t_R \geq t_T$. Accordingly, the catch density rate of the tagged fish would then be $c_T(\mathbf{r},t) = N_R\delta(\mathbf{r} - \mathbf{r}_R)\delta(t - t_R)$. Therefore, on substituting those values in (37) and integrating, I can conclude that the difference between the effort-independent and effort-dependent Green functions is no greater than

$$g(\mathbf{r},t|\mathbf{r}_T,t_T) - g_0(\mathbf{r},t|\mathbf{r}_T,t_T) = 5 \times 10^{-2}\, g(\mathbf{r},t|\mathbf{r}_R,t_R)\,.$$

Because $5 \times 10^{-2} \ll 1$, $g \approx g_0$, which in turn implies that the natural death rate is much greater than the fishing death rate. In that limit, (33) becomes

$$c(\mathbf{r},t) \approx f(\mathbf{r},t)\left[\int_{\text{ETA}} d^2\mathbf{r}' g(\mathbf{r},t|\mathbf{r}',t_T)\, p_{\text{in}}(\mathbf{r}') + u(\mathbf{r},t)\right].$$

The catch density rate, under the condition of low fishing death rate in relation to the natural death rate, is approximately a linear function of effort density. Had the tag return been double its reported value, the approximation of catch as a linear function of effort would still hold because $N_R/N_T = 0.1$ is an order of

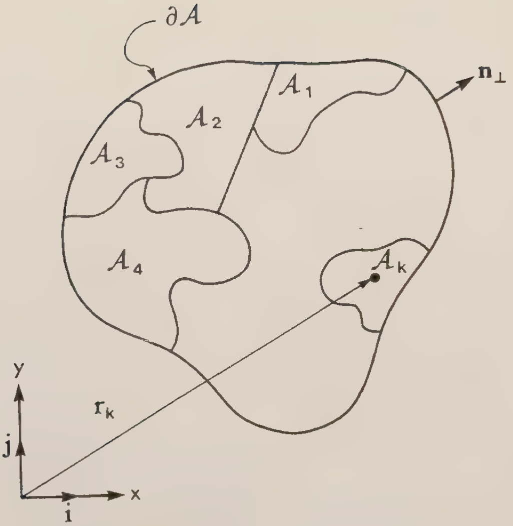

FIG. 2. Domain $\mathcal{A}$ of the population is divided into $n$ nonoverlapping cells. The vector $\mathbf{n}_\perp$ is the unit vector normal to the boundary $\partial\mathcal{A}$ of the domain pointing outward.

magnitude smaller than 1. Should the recruitment density rate not change sigificantly, doubling the effort would have the effect of approximately doubling the catch. Thus, in answer to the Fonteneau question, if the effort in one or more of the five cells were doubled, the catch from the remaining cells would remain approximately constant.

## 5. Discretization of the Fields

Should the fishing death rate approach or exceed the natural death rate, the field equations of Section 3 must be treated in much more detail to address the general fishery problem outlined in Section 2. A numerical solution is proposed in this section.

With reference to Fig. 2, the individual cells of area $\mathcal{A}_i$ of the domain $\mathcal{A}$, where $i = 1, 2, \ldots, n$, are such that

$$\mathcal{A} = \sum_{i=1}^{n} \mathcal{A}_i$$

(i.e., no overlap of cells), and $\{\mathbf{r}_i \in \mathcal{A}_i : i = 1, 2, \ldots, n\}$. Here, cell $\mathcal{A}_i$ is defined as a neighborhood around point (or nuclei) $\mathbf{r}_i$. A cell is defined about every data collection nucleus. An economic zone can be composed of more than one cell. The closed time interval $\mathcal{T}_T = [t_T,t] = [t_l,t_{m+1}]$, where $l \geq 1$ and the equality holds only if $\mathcal{T}_T = \mathcal{T}_l$. The $m$ time intervals $\{\mathcal{T}_j = t_{j+1} - t_j : j = 1, 2, \ldots, m\}$ are such that

$$\mathcal{T}_l = \sum_{j=1}^{m} \mathcal{T}_j = [t_1, t_{m+1}] \,.$$

The value of a field $\phi$ within cell $\mathcal{A}_i$ in the interval of time $\mathcal{T}_j = [t_j,t_{j+1}]$ will be written $\phi(\mathbf{r}_i,t_j)$. Henceforth, $(\mathbf{r}_i,t_j)$ is interchangeable with $(\mathcal{A}_i,\mathcal{T}_j)$.

I will assume that $N_T$ number of tagged fish are released in cell $\mathcal{A}_k$ at time $t_l$. The following discrete fields are available for the analysis: $\mathcal{E} = [e(\mathbf{r}_i,t_j) : i = 1, 2, \ldots, n; j = 1, 2, \ldots, m + 1\}$, $\mathcal{C} = \{c(\mathbf{r}_i,t_j) : i = 1, 2, \ldots, n; j = 1, 2, \ldots, m + 1\}$, and $\mathcal{C}_T(\mathbf{r}_k,t_l) = \{c_T(\mathbf{r}_i,t_j) : i = 1, 2, \ldots, n; j = l, l + 1, \ldots, m + 1\}$. These are, respectively, the measurements of effort density, the untagged fish catch density rate, and tagged fish catch density rate for the release of tagged fish in cell $\mathcal{A}_k$ at time $t_l$. It will soon become evident that at the very least there should be as many tagging experiments as there are cells in the domain, one per cell.

As I showed in Section 3, I first need to evaluate the catchability in order to construct the effort-dependent Green function. The discrete version of (23) is

$$(45)\quad q(\mathbf{r}_v,t_s) = \frac{1}{N_T(r_v,t_s)} \sum_{i=1}^{n} \mathcal{A}_i \frac{c_T(\mathbf{r}_i,t_s)}{e(\mathbf{r}_i,t_s)} \,.$$

However, by its very definition, I can calculate only one value of $q$ from every tagging experiment. If the tagged fish release is only at $(\mathbf{r}_k,t_l)$, then I can only calculate $q(\mathbf{r}_k,t_l)$. So in the case of the single tagging experiment, I am left with the necessity of assuming $q$ constant throughout space–time.

The discrete version of (22) for $g_0$ for a tagged fish release at $(\mathbf{r}_k,t_l)$ is

$$(46)\quad g_0(\mathbf{r}_i,t_j|\mathbf{r}_k,t_l) = \frac{c_T(\mathbf{r}_i,t_j)}{q(\mathbf{r}_i,t_j)\, e(\mathbf{r}_i,t_j)\, N(\mathbf{r}_k,t_l)} \,.$$

If only the one tagging experiment has been performed, then, as mentioned above, it is necessary to assume $q(\mathbf{r}_i,t_j) = q(\mathbf{r}_k,t_l) =$ constant for $i = 1, 2, \ldots, n$ and $j = l, l + 1, \ldots, m + 1$. Thus, using the set $\mathcal{C}_T$ of a single tagging experiment and set $\mathcal{E}$, I can construct an approximate $g_0$. The set of values calculated for $g_0$ for a release of fish at $(\mathbf{r}_k,t_l)$ will be called the set $\mathcal{G}_0(\mathbf{r}_k,t_l) = \{g_0(\mathbf{r}_i,t_{l+s}|\mathbf{r}_k,t_l) : i = 1, 2, \ldots, n; s = 1, 2, \ldots, m - l + 1\}$. To describe the elements of $\mathcal{G}_0(\mathbf{r}_k,t_l)$, it is helpful to use the Kroenecker delta function:

$$\delta_{ik} = \begin{cases} 1 & \text{if } i = k \\ 0 & \text{otherwise} \,. \end{cases}$$

Then

$$g_0(\mathbf{r}_i,t_j|\mathbf{r}_k,t_l) = \begin{cases} 0 & \text{for } t_j < t_l \\ \delta_{ik}/\mathcal{A}_k & \text{for } t_j = t_l \end{cases}$$

and

$$g_0(\mathbf{r}_i,t_j|\mathbf{r}_k,t_l) \leq \delta_{ik}/\mathcal{A}_k \quad \text{for } t_j > t_l \,.$$

As a consequence of this last property, for $t_j \geq t_l$ :

$$0 \leq \sum_{i=1}^{n} \mathcal{A}_i\, g_0(\mathbf{r}_i,t_j|\mathbf{r}_k,t_l) \leq 1 \,.$$

The discrete version of (37) is given by

$$g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_l) \approx g_0(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_l) + \frac{1}{N_T(\mathbf{r}_k,t_l)}$$

$$\times \sum_{s=1}^{j\leq m} \mathcal{T}_s \sum_{\nu=1}^{n} \mathcal{A}_\nu\, g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_\nu,t_s)\, c_T(\mathbf{r}_\nu,t_s) \,.$$

Therefore, for an arbitrary single interval of time, say $\mathcal{T}_j$, the relationship between $g$ and $g_0$ is

$$(47) \quad g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j) \approx g_0(\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j) + \frac{\mathcal{T}_j}{N_T(\mathbf{r}_w,t_j|\mathbf{r}_k,t_l)}$$

$$\times \sum_{\nu=1}^{n} \mathcal{A}_\nu\, g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_\nu,t_j)\, c_T(\mathbf{r}_\nu,t_j)$$

where $N(\mathbf{r}_w,t_j|\mathbf{r}_k, t_l)$ is the number of tagged fish at $(\mathbf{r}_w,t_j)$ from a release conducted at $(\mathbf{r}_k,t_l)$. From (18), this is

$$N_T(\mathbf{r}_w,t_j|\mathbf{r}_k,t_l) = \mathcal{A}_w\, p_T(\mathbf{r}_w,t_j) = \mathcal{A}_w\, g_0(\mathbf{r}_w,t_j|\mathbf{r}_k,t_l)\, N_T(\mathbf{r}_k,t_l) \,.$$

The exact solution of (47) is given by the series

$$(48) \quad g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j) = \sum_{r=0}^{\infty} g_r(\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j)$$

and

$$g_r(\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j) \approx \frac{\mathcal{T}_j}{N_T(\mathbf{r}_w,t_j|\mathbf{r}_k,t_l)} \sum_{\nu=1}^{n} \mathcal{A}_\nu\, g_{r-1}(\mathbf{r}_i,t_{j+1}|\mathbf{r}_\nu,t_j)\, c_T(\mathbf{r}_\nu,t_j)$$

for $r = 1, 2, \ldots$. For cases where $m \not\ll f$, that is, if the number of tagged fish recaptured in the interval of time $\mathcal{T}_j$ is

$$N_R(t_{j+1}) \approx \mathcal{T}_j \sum_{i=1}^{n} \mathcal{A}_i\, c_T(\mathbf{r}_i,t_j) \,.$$

the approximation

$$g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j) \approx g_0(\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j) + \frac{\mathcal{T}_j}{N_T(\mathbf{r}_w,t_j|\mathbf{r}_k,t_l)}$$

$$\times \sum_{\nu=1}^{n} \mathcal{A}_\nu\, g_0(\mathbf{r}_i,t_{j+1}|\mathbf{r}_\nu,t_j)\, c_T(\mathbf{r}_\nu,t_j)$$

will give accurate results if $N_R < N_T$ but $N_R \not\ll N_T$. As I mentioned in Section 3, if $N_R \ll N_T$, implying that natural death rate is much greater than that due to fishing, then the approximation $g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j) \approx g_0\, (\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j)$ is adequate. However, in general, one can proceed by expanding and stop the expansion with the term whose contribution is negligible.

Either the exact or approximate solution for $g$ requires the knowledge of the transition probability density elements $\mathcal{G}_0^* = \{g_0(\mathbf{r}_i,t_{j+1}|\mathbf{r}_\nu,t_j) : i, \nu = 1, 2, \ldots, n; j = l, l+1, \ldots, m\}$. For tagged fish releases starting in the interval of time $\mathcal{T}_l$ the empirical construction of $g_0$ by (46) yields only $\mathcal{G}_0(\mathbf{r}_k,t_l)$. So it is necessary to calculate the transition probability density elements. This will be done with the property of superposition of probability densities (Property G in Section 3).

The discrete version of the superposition property of probability densities for consecutive time intervals is given by

$$(49) \quad g_0(\mathbf{r}_i,t_{l+2}|\mathbf{r}_k,t_l) \approx \sum_{\nu+1}^{n} \mathcal{A}_\nu\, g_0(\mathbf{r}_i,t_{l+2}|\mathbf{r}_\nu,t_{l+1})\, g_0(\mathbf{r}_\nu,t_{l+1}|\mathbf{r}_k,t_l) \,.$$

In order to define a completely determined system of equations for the transition probability densities $\mathcal{G}_0^*(\mathcal{T}_{l+1}) = \{g_0(\mathbf{r}_i,t_{l+2}|\mathbf{r}_\nu,t_{l+1}) : i, \nu = 1, 2, \ldots, n\}$ from the information of a single tagging experiment, it is necessary to assume that the Green function is spatially translationally invariant. That is, it is necessary to assume that no matter where the tagged fish are released, the results are identical. However, the concept of translational invariance of the Green function is incompatible with the presence of boundaries, for the results of a tagged fish release away from the boundaries, for example, will be different from the results if the release were close to a boundary. Furthermore, fishing effort is not uniform throughout $\mathcal{A}$. Thus, one cannot possibly define a completely determined system of equations for the transition probability densities $\mathcal{G}_0^*(\mathcal{T}_{l+1})$ from the information of a single tagging experiment if the population has a bounded domain or there is an inhomogeneous distribution of fishing death rate. Investigation of (49) leads to the conclusion that at least $n$ tagging experiments are necessary to perform, one per cell, to define a completely determined system of equations. As can be appreciated in (49), if $n$ simultaneous tagged fish releases were done, one per cell, the data at the initial interval of time and all subsequent intervals define completely determined systems of $n$ equations. However, it is not necessary to perform the tagged fish releases simultaneously. To see this, it is best to consider an example.

For simplicity, I will suppose that the release at time $t_l$ is in cell $\mathcal{A}_1$, the release at time $t_{l+1}$ is in cell $\mathcal{A}_2, \ldots$, and the release at time $t_{l+n-1}$ is in cell $\mathcal{A}_n$. To determine the complete set of transition probability densities for an interval of time, it is necessary that there be as many tagging experiments as there are cells in the domain, one per cell, but it is sufficient that there be only one experiment per interval of time. Some or all can be done simultaneously. With the catch data of each experiment, because I have assumed distinguishable tags, one has the set of sets $\mathcal{C}_T = \{\mathcal{C}_T(\mathbf{r}_s,t_{l+s-1}) : s = 1, 2, \ldots, n\}$, that is, the set of catch density rates of the $n$ tagging experiments. Use of $\mathcal{E}$ and $\mathcal{C}_T$ in equation (45) will yield a set of computed catchabilities given by $\mathcal{Q} = \{q(\mathbf{r}_s,t_{l+s-1}) : s = 1, 2, \ldots, n\}$. I can use these to compute a set of discrete Green functions $\mathcal{G}_0 = \{\mathcal{G}_0(\mathbf{r}_s,t_{l+s-1}) : s = 1, 2, \ldots, n\}$ as indicated by (46). However, the catchability of the $i$th cell at time $t_j$ should be used for the computation of terms of all $n$ Green functions evaluated in the $i$th cell (i.e., receiver point $\mathbf{r}_i$) at time $t_j$.

Assuming the tagged fish live longer than $[t_l,t_{l+n}]$, the second transition when there is data from all $n$ tagging experiments is during interval of time $\mathcal{T}_{l+n}$. I am arbitrarily using the transitions at $\mathcal{T}_{l+n}$ rather than those at $\mathcal{T}_{l+n-1}$ for the sake of uniformity of notation in the analysis that follows. From (49), for the release of tagged fish in $\mathcal{A}_1$:

$$g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_1,t_l) \approx \sum_{\nu=1}^{n} \mathcal{A}_\nu\, g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_\nu,t_{l+n})\, g_0(\mathbf{r}_\nu,t_{l+n}|\mathbf{r}_1,t_l) \,.$$

For the release of tagged fish in $\mathcal{A}_2$:

$$g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_2,t_{l+1}) \approx \sum_{v=1}^{n} \mathcal{A}_v\, g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_v,t_{l+n})\, g_0(\mathbf{r}_v,t_{l+n}|\mathbf{r}_2,t_{l+1})$$

$$\vdots$$

and finally, for the release of tagged fish in $\mathcal{A}_n$:

$$g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_n,t_{l+n-1}) \approx \sum_{v=1}^{n} \mathcal{A}_v\, g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_v,t_{l+n})\, g_0(\mathbf{r}_v,t_{l+n}|\mathbf{r}_n,t_{l+n-1}) .$$

This is a system of equations of the form

$$(50) \quad \mathbf{d}_s = \sum_{v=1}^{n} \mathcal{P}_{sv}\, \mathbf{m}_v \text{ for } s = 1, 2, \ldots, n .$$

In this equation, identify by comparison with (49)

$$\mathbf{d} = \begin{pmatrix} g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_1,t_l) \\ g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_2,t_{l+1}) \\ \cdot \\ g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_n,t_{l+n-1}) \end{pmatrix}$$

as the data vector,

$$\mathcal{P} = \begin{pmatrix} \mathcal{A}_1 g_0(\mathbf{r}_1,t_{l+n}|\mathbf{r}_1,t_l) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_{l+n}|\mathbf{r}_1,t_l) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_{l+n}|\mathbf{r}_1,t_l) \\ \mathcal{A}_1 g_0(\mathbf{r}_1,t_{l+n}|\mathbf{r}_2,t_{l+1}) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_{l+n}|\mathbf{r}_2,t_{l+1}) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_{l+n}|\mathbf{r}_2,t_{l+1}) \\ \cdot & \cdot & \cdot & \cdot \\ \mathcal{A}_1 g_0(\mathbf{r}_1,t_{l+n}|\mathbf{r}_n,t_{l+n-1}) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_{l+n}|\mathbf{r}_n,t_{l+n-1}) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_{l+n}|\mathbf{r}_n,t_{l+n-1}) \end{pmatrix}$$

as the $n \times n$ matrix of coefficients, and

$$\mathbf{m} = \begin{pmatrix} g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_1,t_{l+n}) \\ g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_2,t_{l+n}) \\ \cdot \\ g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_n,t_{l+n}) \end{pmatrix}$$

as the model vector. Solving this system of equations for $i = 1, 2, \ldots, n$ gives the set $\mathcal{G}_0^*(\mathcal{T}_{l+n}) = \{g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_v,t_{l+n}) : i, v = 1, 2, \ldots, n\}$. Following the previous procedure for the next time step (i.e., $\mathcal{T}_{l+n+1}$), solve (50) with

$$\mathbf{d} = \begin{pmatrix} g_0(\mathbf{r}_i,t_{l+n+2}|\mathbf{r}_1,t_l) \\ g_0(\mathbf{r}_i,t_{l+n+2}|\mathbf{r}_2,t_{l+1}) \\ \cdot \\ g_0(\mathbf{r}_i,t_{l+n+2}|\mathbf{r}_n,t_{l+n-1}) \end{pmatrix}$$

as the data vector,

$$\mathcal{P} = \begin{pmatrix} \mathcal{A}_1 g_0(\mathbf{r}_1,t_{l+n+1}|\mathbf{r}_1,t_l) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_{l+n+1}|\mathbf{r}_1,t_l) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_{l+n+1}|\mathbf{r}_1,t_l) \\ \mathcal{A}_1 g_0(\mathbf{r}_1,t_{l+n+1}|\mathbf{r}_2,t_{l+1}) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_{l+n+1}|\mathbf{r}_2,t_{l+1}) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_{l+n+1}|\mathbf{r}_2,t_{l+1}) \\ \cdot & \cdot & \cdot & \cdot \\ \mathcal{A}_1 g_0(\mathbf{r}_1,t_{l+n+1}|\mathbf{r}_n,t_{l+n-1}) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_{l+n+1}|\mathbf{r}_n,t_{l+n-1}) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_{l+n+1}|\mathbf{r}_n,t_{l+n-1}) \end{pmatrix}$$

as the matrix of coefficients, and

$$\mathbf{m} = \begin{pmatrix} g_0(\mathbf{r}_i,t_{l+n+2}|\mathbf{r}_1,t_{l+n+1}) \\ g_0(\mathbf{r}_i,t_{l+n+2}|\mathbf{r}_2,t_{l+n+1}) \\ \cdot \\ g_0(\mathbf{r}_i,t_{l+n+2}|\mathbf{r}_n,t_{l+n+1}) \end{pmatrix}$$

as the model vector. Its solution for $i = 1, 2, \ldots, n$ will yield the set $\mathcal{G}_0^*(\mathcal{T}_{l+n+1}) = \{g_0(\mathbf{r}_i,t_{l+n+2}|\mathbf{r}_v,t_{l+n+1}) : i, v = 1, 2, \ldots, n\}$. Proceeding successively to the last system of equations, which in the interval of time $\mathcal{T}_m$, are given by

$$\mathbf{d} = \begin{pmatrix} g_0(\mathbf{r}_i,t_{m+1}|\mathbf{r}_1,t_l) \\ g_0(\mathbf{r}_i,t_{m+1}|\mathbf{r}_2,t_{l+1}) \\ \\ g_0(\mathbf{r}_i,t_{m+1}|\mathbf{r}_n,t_{l+n-1}) \end{pmatrix}$$

as the data vector,

$$\mathcal{P} = \begin{pmatrix} \mathcal{A}_1 g_0(\mathbf{r}_1,t_m|\mathbf{r}_1,t_l) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_m|\mathbf{r}_1,t_l) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_m|\mathbf{r}_1,t_l) \\ \mathcal{A}_1 g_0(\mathbf{r}_1,t_m|\mathbf{r}_2,t_{l+1}) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_m|\mathbf{r}_2,t_{l+1}) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_m|\mathbf{r}_2,t_{l+1}) \\ \cdot & \cdot & \cdot & \cdot \\ \mathcal{A}_1 g_0(\mathbf{r}_1,t_m|\mathbf{r}_n,t_{l+n-1}) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_m|\mathbf{r}_n,t_{l+n-1}) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_m|\mathbf{r}_n,t_{l+n-1}) \end{pmatrix}$$

as the matrix of coefficients, and

$$\mathbf{m} = \begin{pmatrix} g_0(\mathbf{r}_i,t_{m+1}|\mathbf{r}_1,t_m) \\ g_0(\mathbf{r}_i,t_{m+1}|\mathbf{r}_2,t_m) \\ \cdot \\ g_0(\mathbf{r}_i,t_{m+1}|\mathbf{r}_n,t_m) \end{pmatrix}$$

as the model vector. Solving these for $i = 1, 2, \ldots, n$ will yield the set $\mathcal{G}_0^*(\mathcal{T}_m) = \{g_0(\mathbf{r}_i,t_{m+1}|\mathbf{r}_v,t_m) : i, v = 1, 2, \ldots, n\}$. Any number of numerical techniques can be used to solve (49), or the integral equations of Section 3 for those cases in which an analytical model is chosen (Franklin 1970; Tikhonov and Arsenin 1977; Lavrentev et al. 1986; Parker 1990; Wahba 1990; Press et al. 1992). For noisy data characteristic of fisheries, stable solutions resulting from the inversion of the above systems of equations will have the effect of smoothing the solutions at the expense of resolution. In the end of this process of solving these $m - l - n$ systems of $n$ equations, I will have constructed the set $\mathcal{G}_0^* = \mathcal{G}_0^*(\mathcal{T}_{l+n}) \cup \mathcal{G}_0^*(\mathcal{T}_{l+n+1}) \cup \ldots \cup \mathcal{G}_0^*(\mathcal{T}_m) = \{\mathcal{G}_0^*(\mathcal{T}_j) : j = l + n, l + n + 1, \ldots, m\} = \{g_0(\mathbf{r}_i, t_{j+1}|\mathbf{r}_v, t_j) : i, v = 1, 2, \ldots, n; = l + n, l + n + 1, \ldots, m\}$ necessary to generate the set $\mathcal{G}^* = \{g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_v,t_j) : i, v = 1, 2, \ldots, n; j = l + n, l + n + 1, \ldots, m\}$ of effort-independent transition probability densities by use of (48).

If the population exhibits periodic behavior of period $\mathcal{T} < t_{m+1} - t_{l+n}$, then some of the transitions will be repeated because

$$g_0(\mathbf{r}_i,t_{j+1}|\mathbf{r}_v,t_j) = g_0(\mathbf{r}_i,t_{j+1} + \mathcal{T}\,|\mathbf{r}_v,t_j + \mathcal{T}\,) .$$

It is desirable that tagged fish persist in their domain as long as possible but at least for two periods. This means that, in general, some transitions will have more than one value, one for each period that the tagged fish persist in their domain and there is catch of tagged fish. Due to statistical fluctuations, they will be generally unequal and can be averaged.

Natural periods, such as seasonal, are at best approximate. Due to the inherently stochastic nature of fish movement, the approximate repetition of their seasonal movement may be advanced or retarded. However, the transition probability densities may help decide the duration of a period by the consistent lack or peaks of a subset of $\mathcal{G}^*$, the set of effort-independent transition probability densities. For the estimation of periods the set $\mathcal{G}_0^*$ should not be used because some of the periodic nature of its subsets could be due to seasonal application of fishing effort.

Once the set $\mathcal{G}^*$ of effort-independent transition probability density elements for the fish dynamics are determined, they can be used to determine the contribution to the population density due to recruitment. The discrete version of (44) for a single time interval is

$$(51) \quad u(\mathbf{r}_i,t_{j+1}) \approx \frac{c(\mathbf{r}_i,t_{j+1})}{q(\mathbf{r}_i,t_{j+1}\; e(\mathbf{r}_i,t_{j+1})} - \sum_{v=1}^{n} \mathcal{A}_v g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_v,t_j) \times \left[\frac{1}{f(\mathbf{r}_v,t_j)} - \mathcal{T}_j\right] c(\mathbf{r}_v,t_j) .$$

Because I have sets $\mathcal{C}$, $\mathcal{Q}$, $\mathcal{E}$, and $\mathcal{G}^*$, I can compute with (51) the set $\mathcal{U} = \{u(\mathbf{r}_i,t_{j+1}) : i = 1, 2, \ldots, n; j = l + n, l + n + 1, \ldots, m\}$. To compute the catch density rate $\mathcal{C}' = \{c'(\mathbf{r}_i,t_{j+1}) : i = 1, 2, \ldots, n; j = l + n, l + n + 1, \ldots, m\}$ at a new level of effort density $\mathcal{E}' = \{e'(\mathbf{r}_i, t_{j+1}) : i = 1, 2, \ldots, n; j = l + n, l + n + 1, \ldots, m\}$, the population density at the different level of effort density can be computed with the discretized version of (41) which for a single interval of time $\mathcal{T}_j$ is given by

$$(52) \quad p'(\mathbf{r}_i,t_{j+1}) \approx \sum_{v=1}^{n} \mathcal{A}_v g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_v,t_j)\,[1 - \mathcal{T}_j\, q(\mathbf{r}_v,t_j) \times e'(\mathbf{r}_v,t_j)]\, p(\mathbf{r}_v,t_j) + u(\mathbf{r}_i,t_{j+1})$$

and is applied recursively for $j = l + n, l + n + 1, \ldots, m$. In (52), one assumes that the recruitment density rate does not change significantly at the new level of effort. The catch density rate $\mathcal{C}'$ at the different level of effort density $\mathcal{E}'$ is computed by multiplying the result of (52) by $q(\mathbf{r}_i,t_{j+1})e'(\mathbf{r}_i,t_{j+1})$.

To summarize the previous example, the following steps must be taken to solve the fisheries interaction problem:

1. Using the set of tagged fish catch density rates of $n$ tagging experiments ($\mathcal{C}_T$) and the set of effort density measurements ($\mathcal{E}$), the set of catchabilities ($\mathcal{Q}$) is constructed by use of (45). There will be one catchability associated with each cell and interval of time where tagged fish are released. If only one tagging experiment is conducted in each cell, then one is forced to assume that the value of each catchability in each cell is time independent.

2. Using the sets $\mathcal{C}_T$, $\mathcal{E}$, and $\mathcal{Q}$, the set of discrete Green functions ($\mathcal{G}_0$) for the $n$ tagging experiments is constructed by use of (46).

3. The set of effort-dependent transition probability densities ($\mathcal{G}_0^*$) is constructed by application of $\mathcal{G}_0$ to (49).

4. The set of effort-independent transition probability densities ($\mathcal{G}^*$) is constructed by application of $\mathcal{G}_0^*$ to (48).

5. With the set of catch density rates of untagged fish ($\mathcal{C}$) and sets $\mathcal{Q}$, $\mathcal{E}$, and $\mathcal{G}^*$, the set of population densities due to recruitment $\mathcal{U}$ is constructed by applying (51).

6. Assuming a new level of effort given by the set $\mathcal{E}' \neq \mathcal{E}$, the resulting catch $\mathcal{C}'$ is computed using $\mathcal{E}'$, $\mathcal{Q}$, and $\mathcal{U}$ in (52) and multiplying the population densities $p'(\mathbf{r}_i,t_{j+1})$ by $f(\mathbf{r}_i,t_{j+1}) = q(\mathbf{r}_i,t_{j+1})e'(\mathbf{r}_i,t_{j+1})$.

The recruitment density rate $\mathcal{R} = \{r(\mathbf{r}_i,t_j) : i = 1, 2, \ldots, n; j = l + n, l + n + 1, \ldots, m\}$ is computed by inversion of the system by inversion of the system of equations

$$u(\mathbf{r}_i,t_{j+1}) \approx \mathcal{T}_j \sum_{\nu=1}^{n} \mathcal{A}_\nu g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_\nu,t_j)\, r(\mathbf{r}_\nu,t_j)\,.$$

which is the discretized field $u(\mathbf{r},t)$ given in (42) for a single time interval $\mathcal{T}_j$. For this system of equations, identify in (50)

$$\mathbf{d} = \begin{pmatrix} u(\mathbf{r}_1,t_{j+1}) \\ u(\mathbf{r}_2,t_{j+1}) \\ \cdot \\ u(\mathbf{r}_n,t_{j+1}) \end{pmatrix}$$

as the data vector,

$$\mathcal{P} = \mathcal{T}_j \begin{pmatrix} \mathcal{A}_1 g(\mathbf{r}_1,t_{j+1}|\mathbf{r}_1,t_j) & \mathcal{A}_2 g(\mathbf{r}_1,t_{j+1}|\mathbf{r}_2,t_j) & \cdot & \mathcal{A}_n g(\mathbf{r}_1,t_{j+1}|\mathbf{r}_n,t_j) \\ \mathcal{A}_1 g(\mathbf{r}_2,t_{j+1}|\mathbf{r}_1,t_j) & \mathcal{A}_2 g(\mathbf{r}_2,t_{j+1}|\mathbf{r}_2,t_j) & \cdot & \mathcal{A}_n g(\mathbf{r}_2,t_{j+1}|\mathbf{r}_n,t_j) \\ \cdot & \cdot & \cdot & \cdot \\ \mathcal{A}_1 g(\mathbf{r}_n,t_{j+1}|\mathbf{r}_1,t_j) & \mathcal{A}_2 g(\mathbf{r}_n,t_{j+1}|\mathbf{r}_2,t_j) & \cdot & \mathcal{A}_n g(\mathbf{r}_n,t_{j+1}|\mathbf{r}_n,t_j) \end{pmatrix}$$

as the $n \times n$ matrix of coefficients, and

$$\mathbf{m} = \begin{pmatrix} r(\mathbf{r}_1,t_j) \\ r(\mathbf{r}_2,t_j) \\ \cdot \\ r(\mathbf{r}_n,t_j) \end{pmatrix}$$

as the model vector. The system of equations must be solved for the $j = l + n, l + n + 1, \ldots, m$ time intervals. However, in order to be able to accurately resolve the population density due to recruitment from the population at large by use of (51), it is essential that the Green function also be a measure of the survivability and movement of the untagged portion of the population. As has been discussed before, this condition is true only if sufficient numbers of tagged fish are released.

Once the recruitment density rate is resolved from the above inversions, I am free to interpret it as a nonlinear function of population density. The same result is achieved by inverting for the recruitment density rate using the corresponding algebraic equations that involve the effort-dependent Green function.

## 6. Estimation of the Field Equation Coefficients

In this section, I will show how to calculate the coefficients of the field equation using tagged fish data. This method is a modification of an analytical technique that is used to construct solutions of stochastic differential equations from Fokker–Planck equations (Okubo 1980; Zwillinger 1989) by the use of moments. The modification developed here will lead to the identification of a closed-form expression for the transition probability densities for small intervals of time. I will show that because the moment method is unable to resolve the divergence of the drift velocity and the Laplacian of the diffusivity, I am left with two alternative models that do equally well interpreting the data.

I assume that I have resolved a smooth set $\mathcal{G}^*$ of the effort-independent transition probability density elements. However, this analysis can also be done with $\mathcal{G}_0^*$. The Green function of the dynamics the population follows is given by

$$\left[\frac{\partial}{\partial t} + \mathcal{L}\right] g(\mathbf{r},t|\mathbf{r}',t') = \delta(\mathbf{r} - \mathbf{r}')\,\delta(t - t') \tag{53}$$

in the space–time domain $\mathbf{r} \in \mathcal{A}$, where operator $\mathcal{L}$ is

$$\mathcal{L} = b_0(\mathbf{r},t) + \mathbf{b}_1(\mathbf{r},t) \cdot \nabla + b_2(\mathbf{r},t)\,\Delta$$

subject to causality condition

$$g(\mathbf{r},t|\mathbf{r}',t') = 0 \text{ if } t < t'$$

and boundary conditions

$$g(\mathbf{r},t|\mathbf{r}',t') = 0$$

for $\mathbf{r} \in \partial\mathcal{A}_A$ and

$$\mathbf{n}_\perp \cdot \nabla g(\mathbf{r},t|\mathbf{r}',t') = 0$$

for $\mathbf{r} \in \partial\mathcal{A}_R$. The only difference between this field equation and (7) is that here, $b_0(\mathbf{r},t) = m(\mathbf{r},t) + \nabla \cdot \mathbf{v}(\mathbf{r},t)$.

The even moments of $g$ are found by multiplying (53) by $r^{2N}$ and integrating over space $\mathcal{A}$ in the interval of time $\mathcal{T}_{-\infty} = [-\infty,t]$. Once these integrations are performed, space–time discretization of the resulting equation for a single interval of time and invoking the initial property of $g$, for a source in cell $\mathcal{A}_k$ in the interval of time $\mathcal{T}_j$, leads to the equation for the $2N$th moment of $g$ (Appendix C) given by

$$(54)\quad r_k^{2N} m(\mathbf{r}_k,t_j) - 2\,N r_k^{2N-2}\,\mathbf{r}_k \cdot \mathbf{v}(\mathbf{r}_k,t_j) - 4\,N^2 r_k^{2N-2} k(\mathbf{r}_k,t_j) - 2\,N r_k^{2N-2}\mathbf{r}_k \cdot \nabla_k\, k(\mathbf{r}_k,t_j) = \frac{1}{\mathcal{T}_j}\left[r_k^{2N} - \langle\, r_i^{2N} \,\rangle\,(t_{j+1}|\mathbf{r}_k,t_j)\right]$$

for $\mathbf{r}_k \notin \partial\mathcal{A}$, where

$$\langle\, r_i^{2N} \,\rangle\,(t_{j+1}|\mathbf{r}_k,t_j) = \sum_{i=1}^{n} \mathcal{A}_i\, r_i^{2N}\, g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_j)\,.$$

The odd moments are calculated by going through the same process after multiplication of the field equation for $g$ by $r^{2N}\mathbf{r}$. The result is (Appendix C)

$$(55)\quad r_k^{2N}\mathbf{r}_k m(\mathbf{r}_k,t_j) - r_k^{2N}\mathbf{v}(\mathbf{r}_k,t_j) - 2\,N r_k^{2N-2}\mathbf{r}_k[\mathbf{r}_k \cdot \mathbf{v}(\mathbf{r}_k,t_j)] - 4\,N(N+1)\, r_k^{2N-2}\mathbf{r}_k\, k(\mathbf{r}_k,t_j)$$

$$- r_k^{2N}\,\nabla_k\, k(\mathbf{r}_k,t_j) - 2\,N r_k^{2N-2}\mathbf{r}_k[\mathbf{r}_k \cdot \nabla_k k(\mathbf{r}_k,t_j)] = \frac{1}{\mathcal{T}_j}\left[r_k^{2N}\mathbf{r}_k - \langle\, r_i^{2N}\mathbf{r}_i \,\rangle\,(t_{j+1}|\mathbf{r}_k,t_j)\right]$$

for $\mathbf{r}_k \notin \partial\mathcal{A}$, where

$$\langle\, r_i^{2N}\,\mathbf{r}_i \,\rangle\,(t_{j+1}|\mathbf{r}_k,t_j) = \sum_{i=1}^{n} \mathcal{A}_i\, r_i^{2N}\mathbf{r}_i\, g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_j)\,.$$

Because data are collected only at the points that are interior to $\mathcal{A}$, I will consider only those source points $\mathbf{r}_k \notin \partial\mathcal{A}$. For points $\mathbf{r}_k \notin \partial\mathcal{A}$, corrections are necessary (Appendix C). However, for the purposes of this work, they are unnecessary.

With the moments of the transition probability densities for a single interval of time $\mathcal{T}_j$, it is not possible to estimate the values of $\nabla_k \cdot \mathbf{v}(\mathbf{r}_k,t_j)$ and $\Delta_k k(\mathbf{r}_k,t_j)$ in cell $\mathcal{A}_k$. As can be appreciated in (54) and (55), the even- and odd-moment equations are independent of these parameters. For the remaining parameters, $\{m(\mathbf{r}_k,t_j), \mathbf{v}(\mathbf{r}_k,t_j), k(\mathbf{r}_k,t_j), \nabla_k k(\mathbf{r}_k,t_j)\}$, there are restrictions to their resolvablility. To see this, construct from the moment equations (54) and (55) a completely determined system of linear equations. Because the even-moment equations are scalar and the odd moments generate two component vector equations, it is only necessary to compute up to the third order moment. It leads to a system of linear algebraic equations

$$\mathbf{d}_s = \sum_{\nu=1}^{6} \mathcal{P}_{s\nu}\,\mathbf{m}_\nu \quad s = 1, 2, \ldots, 6$$

with

$$\mathbf{d} = \frac{1}{\mathcal{T}_j}\begin{pmatrix} 1 - \langle\, 1 \,\rangle\,(t_{j+1}|\mathbf{r}_k,t_j) \\ x_k - \langle\, x_i \,\rangle\,(t_{j+1}|\mathbf{r}_k,t_j) \\ y_k - \langle\, y_i \,\rangle\,(t_{j+1}|\mathbf{r}_k,t_j) \\ r_k^2 - \langle\, r_i^2 \,\rangle\,(t_{j+1}|\mathbf{r}_k,t_j) \\ r_k^2 x_k - \langle\, r_i^2 x_i \,\rangle\,(t_{j+1}|\mathbf{r}_k,t_j) \\ r_k^2 y_k - \langle\, r_i^2 y_i \,\rangle\,(t_{j+1}|\mathbf{r}_k,t_j) \end{pmatrix}$$

as the data vector

$$\mathbf{m} = \begin{pmatrix} m(\mathbf{r}_k,t_j) \\ v_x(\mathbf{r}_k,t_j) \\ v_y(\mathbf{r}_k,t_j) \\ k(\mathbf{r}_k,t_j) \\ \partial k(\mathbf{r}_k,t_j)/\partial x_k \\ \partial k(\mathbf{r}_k,t_j)/\partial y_k \end{pmatrix}$$

as the model vector, and

$$\mathcal{P} = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ x_k & -1 & 0 & 0 & -1 & 0 \\ y_k & 0 & -1 & 0 & 0 & -1 \\ r_k^2 & -2x_k & -2y_k & -4 & -2x_k & -2y_k \\ r_k^2 x_k & -r_k^2 - 2x_k^2 & -2x_k y_k & -8x & -r_k^2 - 2x_k^2 & -2\,x_k y_k \\ r_k^2 y_k & -2x_k y_k & -r_k^2 - 2y_k^2 & -8y & -2x_k y_k & -r_k^2 - 2y_k^2 \end{pmatrix}$$

as the matrix of coefficients. The matrix of coefficients $\mathcal{P}$ has $det\mathcal{P} = 0$. Therefore, the equations are not linearly independent. Keeping natural death rate and diffusion, there are two alternatives regarding the fields $\mathbf{v}$ and $\nabla_k k$ within cell $\mathcal{A}_k$ during the interval of time $\mathcal{T}_j$: either $\mathbf{v}(\mathbf{r}_k, t_j)$ is constant and $\nabla_k k(\mathbf{r}_k,t_j) = 0$ or $\mathbf{v}(\mathbf{r}_k,t_j) = 0$ and $\nabla_k k(\mathbf{r}_k,t_j)$ is constant. In either case, it is only necessary to consider up to the second moment to define a completely determined system of equations. The matrix of coefficients given by

$$\mathcal{P} = \begin{pmatrix} 1 & 0 & 0 & 0 \\ x_k & -1 & 0 & 0 \\ y_k & 0 & -1 & 0 \\ r_k^2 & -2x_k & -2y_k & -4 \end{pmatrix},$$

which has a determinant given by $det\mathcal{P} = -4$, and the data vector given by

$$\mathbf{d} = \frac{1}{\mathcal{T}_j} \begin{pmatrix} 1 - \langle 1 \rangle (t_{j+1} | \mathbf{r}_k, t_j) \\ x_k - \langle x_i \rangle (t_{j+1} | \mathbf{r}_k, t_j) \\ y_k - \langle y_i \rangle (t_{j+1} | \mathbf{r}_k, t_j) \\ r_k^2 - \langle r_i^2 \rangle (t_{j+1} | \mathbf{r}_k, t_j) \end{pmatrix}$$

are sufficient to define uniquely

$$\mathbf{m} = \begin{pmatrix} m(\mathbf{r}_k, t_j) \\ v_x(\mathbf{r}_k, t_j) \\ v_y(\mathbf{r}_k, t_j) \\ k(\mathbf{r}_k, t_j) \end{pmatrix}$$

in the first alternative or

$$\mathbf{m} = \begin{pmatrix} m(\mathbf{r}_k, t_j) \\ \partial k(\mathbf{r}_k, t_j)/\partial x_k \\ \partial k(\mathbf{r}_k, t_j)/\partial y_k \\ k(\mathbf{r}_k, t_j) \end{pmatrix}$$

in the second alternative. Because the moment method cannot resolve the derivatives $\nabla_k \cdot \mathbf{v}(\mathbf{r}_k, t_j)$ and $\Delta_k k(\mathbf{r}_k, t_j)$, either of the alternatives above will interpret the data equally well. In other words, because the divergence of $\mathbf{v}$ and the Laplacian of $k$ are unresolvable by the moment method, the inverse will interpret the data equally well if $\mathbf{v} = b(t_j)$ and $k = a(t_j)$ or $\mathbf{v} = 0$ and $k = a(t_j) - b(t_j)\mathbf{r}_k/2$. This does not mean that the entire domain of the population has $\{m, \mathbf{v}, k\}$ or $\{m, \nabla_k k\}$ that are independent of position. It means that within each cell of the domain, each, in principle, arbitrarily small, the resolved coefficients $\{m, \mathbf{v}, k\}$ or $\{m, \nabla_k k\}$ are constant within an interval of time.

The solution to the system of equations for the case of the first alternative is

$$m(\mathbf{r}_k, t_j) = \frac{1}{\mathcal{T}_j} \left[ 1 - \langle 1 \rangle (t_{j+1} | \mathbf{r}_k, t_j) \right]$$

$$\mathbf{v}(\mathbf{r}_k, t_j) = \frac{1}{\mathcal{T}_j} \left[ \langle \mathbf{r}_i \rangle (t_{j+1} | \mathbf{r}_k, t_j) - \mathbf{r}_k \langle 1 \rangle (t_{j+1} | \mathbf{r}_k, t_j) \right]$$

$$k(\mathbf{r}_k, t_j) = \frac{1}{4\mathcal{T}_j} \left[ \langle r_i^2 \rangle (t_{j+1} | \mathbf{r}_k, t_j) - 2\mathbf{r}_k \cdot \langle \mathbf{r}_i \rangle (t_{j+1} | \mathbf{r}_k, t_j) \right.$$

$$\left. + r_k^2 \langle 1 \rangle (t_{j+1} | \mathbf{r}_k, t_j) \right].$$

These are the same results, linearized in $\mathcal{T}_j$, that the discrete transition probability density

$$(56) \quad g(\mathbf{r}_i, t_{j+1} | \mathbf{r}_k, t_j) = \exp\left[-\mathcal{T}_j \, m(\mathbf{r}_k, t_j)\right] \mathcal{N}\left(\mathbf{r}_k + \mathcal{T}_j \, \mathbf{v}(\mathbf{r}_k, t_j), \sigma^2\right)$$

where

$$\sigma^2 = 2\,\mathcal{T}_j \, k(\mathbf{r}_k, t_j)$$

(see equation (20)) yields for the unbounded domain when its coefficients are calculated using moments. In fact, (56) yields the moments of $g$ of any order in the interval of time $\mathcal{T}_j$, but those derived here (Appendix C) are linearized in $\mathcal{T}_j$ due to the discretization of the field equation necessary for the derivation. The fact that the moment equations of this section are correct for either the unbounded domain, or the domains bounded by absorbing and/or reflecting boundaries if $\mathbf{r}_k \notin \partial\mathcal{A}$ (Appendix C), leads to the expectation that the closed-form transition probability (56) is also correct for the bounded domain of this work. Because $\mathcal{T}_j$ is small, the transition probability densities are very nearly Dirac delta functions, so for points $\mathbf{r}_i$ not near $\mathbf{r}_k$ the distributions are nearly vanishing.

Finally, transforming (56) with the transformation $m(\mathbf{r}_k, t_j) \rightarrow m(\mathbf{r}_k, t_j) + f(\mathbf{r}_k, t_j)$ yields the closed-form expression for the effort-dependent transition probability densities. These results, coupled with the discrete equations of Section 5, simplify considerably numerical analysis and simulations for an interval of time of arbitrary length. This method should be applicable to problems whose field equation has a Green function with a probabilistic interpretation: Fokker–Planck equations, but more generally, any linear field equation with at most a first-order time derivative but spatial derivatives of arbitrary order. As can be seen by comparing (20) with (56), it is only necessary to find the Green function associated with the field equation that is invariant under space–time translations, and then expressions for small intervals of time for the discrete transition probability densities associated with the corresponding field equation that is not invariant under space–time translations are constructed by inspection. In general, it is only possible to construct exact closed-form expressions for the transition probability densities if the differential operator has spacial derivatives no higher than fourth order.

## 7. Summary

When members of a population are released in an area small compared with their domain and over an interval of time short compared with the length of time they take to disperse throughout their domain, the pattern of movement approximates a point-source solution (or Green function) of the underlying population dynamics. The Green functions, one for each release, can be empirically determined with the mark and recapture data of tagged members of the population with distinguishable tags. The assumed field equations for the population dynamics were inverted to represent the solution in terms of integral equations for the tagged and untagged portions of the population.

Because for a fish population it is necessary to use catch per unit effort of tagged fish to construct the Green functions empirically, the resulting point-source solutions are effort dependent and, therefore, not practical for a fishery interaction problem where it is desired to determine the catch resulting from a different level of effort, the field equations were reformulated such that the term containing effort was redefined as an inhomogeneous term of the field equation. This leads to a method of constructing the effort-independent Green function from knowledge of the effort-dependent one.

Discretization of the integral equations was achieved by defining non overlapping cells of arbitrary shape in the neighborhood of each point where data were collected. The integral equations of the theory, upon discretization, result as systems of coupled algebraic equations which for a single interval of time coincide with a Markovian formulation of the exchange of members of the population between the cells of the discretized space.

For every tagging experiment, it is possible to calculate only one catchability at the cell and time of release. However, to be able to determine approximately a complete effort-independent Green function from knowledge of the effort-dependent one in a bounded population domain, it is required that there be as many tagging experiments as there are cells defined in the domain.

The Green functions were interpreted as the tagged fish probability density of surviving movement to the receiver space–time coordinates from the release coordinates. If sufficiently large numbers of tagged fish are released, then the tagged fish dynamics are representative of the population. Both the effort-dependent and effort-independent Green fuctions can be decomposed into transition probability densities for a single interval of time. The transition probability densities can be used to determine the recruitment density rate which, once resolved, can be freely interpreted as a nonlinear function of the population density. The moments of the transition probability densities lead to the evaluation of model parameters and the identification of the closed-form transition probability densities.

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## Appendix A. Representation Theorem for the Population Density

The purpose of this appendix is to derive an integral representation for the population density. I will show that if on the boundary of the population domain the population density satisfies either homogeneous Dirichlet of Neumann conditions, the integral representation for the solution does not contain a boundary integral. The proof is not intended to be rigorous, but follows mathematical procedures well established and elucidated in the literature (Courant and Hilbert 1953; Morse and Feshbach 1953; Garabedian 1964; Gilbarg and Trudinger 1979).

Let the domain of the population $\mathcal{A} \in \mathbf{R}^2$ be bounded by $\partial\mathcal{A} \in \mathbf{R}$. Let $\mathbf{r} = x\mathbf{i} + y\mathbf{j} \in \mathcal{A}$ be the receiver or measuring point with respect to an arbitrarily chosen fixed coordinate system where $\mathbf{i}$ and $\mathbf{j}$ are, respectively, the unit vectors pointing in the $+x$ and $+y$ directions. Let time $t$ be the receiver time. At time $t_I$, there is an initial population whose subsequent dynamics I wish to model. I assume that the dynamics of the population are correctly given by (7):

$$\text{(A1)}\quad \left[\frac{\partial}{\partial t} + \mathcal{L}_0\right] p(\mathbf{r},t) = r(\mathbf{r},t)$$

where

$$\text{(A2)}\quad \mathcal{L}_0\, p(\mathbf{r},t) = b_0(\mathbf{r},t)\, p(\mathbf{r},t) + \mathbf{b}_1(\mathbf{r},t) \cdot \nabla\, p(\mathbf{r}, t)$$
$$+ b_2(\mathbf{r},t)\, \Delta\, p(\mathbf{r},t)\ .$$

In equation (A2) the coefficients $\{b_0, \mathbf{b}_1, b_2\}$ are related to the coefficients $\{z, \mathbf{v}, k\}$ by

$$b_0(\mathbf{r},t) = z(\mathbf{r},t) + \nabla \cdot \mathbf{v}(\mathbf{r},t)$$

$$\text{(A3)}\quad \mathbf{b}_1(\mathbf{r},t) = \mathbf{v}\,(\mathbf{r},t) - \nabla k(\mathbf{r},t)$$

$$b_2(\mathbf{r},t) = -\,k(\mathbf{r},t)$$

where the derivatives $\nabla \cdot \mathbf{v}(\mathbf{r},t)$ and $\Delta k(\mathbf{r},t)$ are finite.

The general problem for the population density can be formulated as follows: the population density $p(\mathbf{r},t)$ satisfies the inhomogeneous field equation (A1) in the space–time domain $\mathbf{r} \in \mathcal{A}$, $t \geq t_I$, subject to initial condition

$$\text{(A4)}\quad p(\mathbf{r},t_I) = p_{\text{in}}(\mathbf{r})$$

in the domain $\mathbf{r} \in \mathcal{A}$. I wish to determine boundary conditions that can be imposed on $\partial\mathcal{A}$ that leads to a unique representation of the solution for $p(\mathbf{r},t)$.

Defining $\mathbf{r}' = x'\mathbf{i} + y'\mathbf{j} \in \mathcal{A}$ as the source point and $t'$ as the source time, the Green function $g_0(\mathbf{r},t|\mathbf{r}',t')$ that is associated with field equation (A1) satisfies field equation

$$\text{(A5)}\quad \left[\frac{\partial}{\partial t} + \mathcal{L}_0\right] g_0(\mathbf{r}, t|\mathbf{r}\,', t\,') = \delta\,(\mathbf{r} - \mathbf{r}\,')\, \delta\,(t - t\,')$$

in the domain $\mathbf{r} \in \mathcal{A}$ and the causality condition

$$g_0(\mathbf{r},t|\mathbf{r}\,',t\,') = 0 \text{ if } t < t\,'$$

in the domain $\mathbf{r} \in \mathcal{A}$. The key to constructing an integral representation of the solution of an initial-boundary value problem for a field is the ability to construct a bilinear function of the field and a Green function associated with it. Because the differential operator associated with field equation (A5) is not self-adjoint, I must consider the adjoint field equation

$$\text{(A6)}\quad \left[-\frac{\partial}{\partial t} + \mathcal{L}_0^*\right] g_0^*(\mathbf{r},t|\mathbf{r}'',t'') = \delta(\mathbf{r} - \mathbf{r}'')\, \delta(t - t'')$$

in the domain $\mathbf{r} \in \mathcal{A}$, where

$$\mathcal{L}_0^*\, g_0^*(\mathbf{r},t|\mathbf{r}'',t'') = b_0(\mathbf{r},t)\, g_0^*(\mathbf{r},t|\mathbf{r}'',t'')$$
$$-\,\nabla \cdot [\mathbf{b}_1(\mathbf{r},t)\, g_0^*(\mathbf{r},t|\mathbf{r}'',t'')] + \Delta[\mathbf{b}_2(\mathbf{r},t)\, g_0^*(\mathbf{r},t|\mathbf{r}'',t'')]$$

subject to the causality condition

$$g_0^*(\mathbf{r},t|\mathbf{r}'',t'') = 0 \text{ if } t > t\ .$$

By definition of the field equation that $g_0^*(\mathbf{r},t|\mathbf{r}',t')$ satisfies, it is the function adjoint to Green function $g_0(\mathbf{r},t|\mathbf{r}',t')$.

Multiplying field equation (A5) by $g_0^*(\mathbf{r},t|\mathbf{r}'',t'')$ and (A6) by $g_0(\mathbf{r},t|\mathbf{r}',t')$, subtracting the former resulting equation from the latter resulting equation, and integrating over the interval of time $[-\infty,\infty]$ and over $\mathcal{A}$ leads, by application of the Divergence Theorem, to

$$g_0^*(\mathbf{r}\,',t\,'|\mathbf{r}'',t'') - g_0(\mathbf{r}'',t''|\mathbf{r}\,',t\,')$$
$$= \int_{t'}^{t''} dt \oint_{\partial\mathcal{A}} dl\, \mathbf{n}_\perp \cdot \mathbf{P}\,[g_0^*(\mathbf{r},t|\mathbf{r}'',t'')|g_0(\mathbf{r},t|\mathbf{r}\,',t\,')]\ .$$

The bilinear function $\mathbf{P}[g_0^*\,(\mathbf{r},t|\mathbf{r}'',t'')|g_0(\mathbf{r},t|\mathbf{r}',t')]$ is given by

$$\text{(A7)}\quad \mathbf{P}[g_o^*(\mathbf{r},t|\mathbf{r}'',t'')|g_0(\mathbf{r},t|\mathbf{r}\,',t\,')] = -\,g_0(\mathbf{r},t|\mathbf{r}\,',t\,')\, \mathbf{b}_1(\mathbf{r},t)$$
$$\times\, g_0^*(\mathbf{r},t|\mathbf{r}'',t'') + g_0(\mathbf{r},t|\mathbf{r}\,',t\,')\, \nabla\, [b_2(\mathbf{r},t)\, g_0^*(\mathbf{r},t|\mathbf{r}'',t'')]$$
$$-\, b_2(\mathbf{r},t)\, g_0^*(\mathbf{r},t|\mathbf{r}'',t'')\, \nabla\, g_0(\mathbf{r},t|\mathbf{r}\,',t\,') + \mathbf{C}$$

where $\mathbf{C}$ is an arbitrary constant. In order that between $g_0$ and its adjoint $g_0^*$ there be the simple reciprocity relation

$$\text{(A8)}\quad g_0^*(\mathbf{r}\,',t\,'|\mathbf{r}'',t'') = g_0(\mathbf{r}'',t''|\mathbf{r}\,',t\,')\ ,$$

it is sufficient that

$$\text{(A9)}\quad \mathbf{n}_\perp \cdot \mathbf{P}[g_0^*(\mathbf{r},t|\mathbf{r}'',t'')|g_0(\mathbf{r},t|\mathbf{r}\,',t\,')] = 0\ .$$

However, because I also demand uniqueness of the solution, it must vanish in such a way that the conditions imposed that lead to (A9) specify the behavior of both $g$ and its adjoint. Not doing so leads to a solution that is not unique. For example, specifying that $g_0(\mathbf{r},t|\mathbf{r}',t')$ satisfy homogeneous Cauchy conditions (i.e., $g_0(\mathbf{r},t|\mathbf{r}',t') = 0$ and $\mathbf{n}_\perp \cdot \nabla g_0(\mathbf{r},t|\mathbf{r}',t') = 0$ for $\mathbf{r} \in \partial\mathcal{A}$ satisfies (A9) but leaves $g_0^*(\mathbf{r},t|\mathbf{r}'',t'')$ arbitrary. However, the boundary conditions

$$\text{(A10)}\quad g_0(\mathbf{r},t|\,\mathbf{r}\,',t\,') = 0$$

and

$$\text{(A11)}\quad g_0^*(\mathbf{r},t|\,\mathbf{r}\,',t\,') = 0$$

or, if $\mathbf{n}_\perp \cdot \mathbf{v}(\mathbf{r},t) = 0$

$$\text{(A12)}\quad \mathbf{n}_\perp \cdot \nabla\, g_0(\mathbf{r},t|\mathbf{r}\,',t\,') = 0$$

and

$$\text{(A13)}\quad \mathbf{n}_\perp \cdot \nabla\, g_0^*(\mathbf{r},t|\mathbf{r}\,',t\,') = 0$$

for $\mathbf{r} \in \partial\mathcal{A}$ result in $g_0$ and $g_0^*$ uniquely specified, and such that the reciprocity relation (A8) holds

Now, as a consequence of (A8), $g_0(\mathbf{r},t|\mathbf{r}',t')$ satisfies the field equation

$$\left[-\frac{\partial}{\partial t'} + \mathcal{L}_0'^*\right] g_0(\mathbf{r},t|\mathbf{r}',t') = \delta(\mathbf{r}-\mathbf{r}')\,\delta(t-t')$$

in the domain $\mathbf{r}' \in \mathcal{A}$, where $\mathcal{L}_0'^*$ is operator $\mathcal{L}_0^*$ under the change of variables $(\mathbf{r},t) \rightarrow (\mathbf{r}',t')$. Therefore, the representation of the solution that satisfies field equation (A1) and initial conditions (A4) is given by

$$\text{(A14)}\quad p(\mathbf{r},t) = \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t_T)\, p_{\text{in}}(\mathbf{r}') + \int_{\mathcal{T}_I} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t')\, r(\mathbf{r}',t') + \int_{\mathcal{T}_I} dt' \oint_{\partial\mathcal{A}} dl'\, \mathbf{n}_\perp \cdot \mathbf{P}[g_0(\mathbf{r},t|\mathbf{r}',t'), p(\mathbf{r}',t')]$$

where the integral with respect to time is in the domain $\mathcal{T}_I$ by virtue of the initial condition and causality. In (A14) the bilinear function $\mathbf{P}[g_0(\mathbf{r},t|\mathbf{r}',t'), p(\mathbf{r}',t')$ is given by

$$\text{(A15)}\quad P[g_0(\mathbf{r},t|\mathbf{r}',t'), p(\mathbf{r}',t')] = -p(\mathbf{r}',t')\mathbf{b}_1(\mathbf{r}',t') \times g_0(\mathbf{r},t|\mathbf{r}',t') + p(\mathbf{r}',t')\,\nabla'[b_2(\mathbf{r}',t')\, g_0(\mathbf{r},t|\mathbf{r}',t')] - b_2(\mathbf{r}',t')\, g_0(\mathbf{r},t|\mathbf{r}',t')\,\nabla' p(\mathbf{r}',t') + \mathbf{C}$$

where $\mathbf{C}$ is an arbitrary constant. Furthermore, because (A8) holds due to boundary conditions (A10) and (A11) or (A12) and (A13), it follows that $g_0(\mathbf{r},t|\mathbf{r}',t')$ satisfies boundary condition

$$\text{(A16)}\quad g_0(\mathbf{r},t|\mathbf{r}',t') = 0$$

or

$$\text{(A17)}\quad \mathbf{n}_\perp \cdot \nabla' g_0(\mathbf{r},t|\mathbf{r}',t') = 0$$

for $\mathbf{r}' \in \partial\mathcal{A}$, and therefore,

$$\text{(A18)}\quad p(\mathbf{r},t) = \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t_T)\, p_{\text{in}}(\mathbf{r}') + \int_{\mathcal{T}_I} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t')\, r(\mathbf{r}',t')$$

is a unique solution of (A1) subject to initial condition (A4) and homogeneous Dirichlet boundary conditions

$$\text{(A19)}\quad p(\mathbf{r},t) = 0$$

or homogeneous Neumann conditions

$$\text{(A20)}\quad \mathbf{n}_\perp \cdot \nabla p(\mathbf{r},t) = 0$$

in the domain $\mathbf{r} \in \partial\mathcal{A}$.

Assume now that the boundary of $\mathcal{A}$ is composed of segments, denoted $\partial\mathcal{A}_A$, on which homogeneous Dirichlet conditions are satisfied, and the remainder of $\partial\mathcal{A}$, denoted $\partial\mathcal{A}_R$, on which the homogeneous Neumann conditions (A20) are satisfied. Proceeding in the same manner as above, the following conclusion can be made: (A18) uniquely satisfies field equation (A1), initial condition (A4), and boundary conditions

$$p(\mathbf{r},t) = 0$$

for $\mathbf{r} \in \partial\mathcal{A}_A$ and

$$\mathbf{n}_\perp \cdot \nabla p(\mathbf{r},t) = 0$$

for $\mathbf{r} \in \partial\mathcal{A}_R$ if $\mathbf{n}_\perp \cdot \mathbf{v}(\mathbf{r},t) = 0$.

## Appendix B. Convergence Condition of the Neumann Expansion

Here, I shall show that the expansion given in (38) converges if the number of tagged fish recovered during an interval of time is less than the number of tagged fish available at the beginning of the interval. To see this, consider the perturbation expansion given in (38):

$$\text{(B1)}\quad g(\mathbf{r},t|\mathbf{r}_T,t_T) = \sum_{i=0}^{\infty} g_i(\mathbf{r},t|\mathbf{r}_T,t_T)$$

where

$$g_i(\mathbf{r},t|\mathbf{r}_T,t_T) = \frac{1}{N_T(\mathbf{r}_T,t_T)} \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g_{i-1}(\mathbf{r},t|\mathbf{r}',t')\, c_T(\mathbf{r}',t')$$

for $i = 1, 2, \ldots$. Presume now that the maximum number of tagged fish recaptured at any one time is $N_M$. Then, I can state the following:

$$c_T(\mathbf{r}',t') \le \frac{N_R}{\mathcal{A}\mathcal{T}_T^2}$$

where $N_R \le N_M\mathcal{T}_T$ is the number of tagged fish recovered in the interval of time $\mathcal{T}_T$. It follows from the probabilistic property of $g_0$ (Property E in Section 3) that there exists a constant $0 \le C \le 1$ such that

$$\int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2r'\, g_0(\mathbf{r},t|\mathbf{r}',t') \le C\mathcal{T}_T.$$

By making use of the first inequality, the iteration relation can be written

$$g_i(\mathbf{r},t|\mathbf{r}_T,t_T) \le \left(\frac{N_R}{N_T(\mathbf{r}_T,t_T)\mathcal{A}}\right)\frac{1}{\mathcal{T}_T^2} \times \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g_{i-1}(\mathbf{r},t|\mathbf{r}',t')$$

for $i = 1, 2, \ldots$, and from which I can compute all terms of the iteration:

$$g_1(\mathbf{r},t|\mathbf{r}_T,t_T) \le \left(\frac{C}{\mathscr{A}\,\mathscr{T}_T}\right)\left(\frac{N_R}{N_T(\mathbf{r}_T,t_T)}\right)$$

$$g_2(\mathbf{r},t|\mathbf{r}_T,t_T) \le \left(\frac{C}{\mathscr{A}\,\mathscr{T}_T}\right)\left(\frac{N_R}{N_T(\mathbf{r}_T,t_T)}\right)^2$$

$$g_N(\mathbf{r},t|\mathbf{r}_T,t_T) \le \left(\frac{C}{\mathscr{A}\,\mathscr{T}_T}\right)\left(\frac{N_R}{N_T(\mathbf{r}_T,t_T)}\right)^N$$

Performing the ratio test

$$\lim_{N\to\infty}\left|\frac{g_{N+1}(\mathbf{r},t|\mathbf{r}_T,t_T)}{g_N(\mathbf{r},t|\mathbf{r}_T,t_T)}\right| = \frac{N_R}{N_T(\mathbf{r}_T,t_T)},$$

which is less than 1 if the number of tagged fish recovered is less than the number of tagged fish released, and therefore, the series converges under that condition.

## Appendix C. Moment Equations of the Green Function

In this appendix, I will find expressions for determining the coefficients of the population field equation by computing the moments of the Green function. I will also show that the inverse problem of determining the coefficients of the field equation in every cell at every interval of time, from the moments of the Green function, leads to nonuniqueness. For source points not on $\partial\mathscr{A}$, the moment equations are correct for either the infinite domain or the domains bounded by a perfectly absorbing and/or perfectly reflecting boundaries. For source points on $\partial\mathscr{A}$, corrections are necessary.

I consider a linear differential operator

$$\mathcal{L} = b_0(\mathbf{r},t) + \mathbf{b}_1(\mathbf{r},t)\cdot\nabla + b_2(\mathbf{r},t)\,\Delta$$

where the coefficients

$$b_0(\mathbf{r},t) = m(\mathbf{r},t) + \nabla\cdot\mathbf{v}(\mathbf{r},t)$$

$$\text{(C1)}\quad \mathbf{b}_1(\mathbf{r},t) = \mathbf{v}(\mathbf{r},t) - \nabla\, k(\mathbf{r},t)$$

$$b_2(\mathbf{r},t) = -\,k(\mathbf{r},t)\,.$$

The derivatives $\nabla\cdot\mathbf{v}(\mathbf{r},t)$ and $\Delta k(\mathbf{r},t)$ are assumed to exist. The effort-independent Green function $g(\mathbf{r},t|\mathbf{r}',t')$ satisfies the field equation

$$\text{(C2)}\quad \left[\frac{\partial}{\partial t} + \mathcal{L}\right] g(\mathbf{r},t|\mathbf{r}',t') = \delta(\mathbf{r}-\mathbf{r}')\delta(t-t')$$

in the space domain $\mathbf{r} \in \mathscr{A}$, subject to the causal condition

$$g(\mathbf{r},t|\mathbf{r}',t') = 0 \text{ if } t < t'\,.$$

The boundary of the domain $\mathscr{A}$ is $\partial\mathscr{A} = \partial\mathscr{A}_A + \partial\mathscr{A}_R$. In terms of the measuring space–time point $(\mathbf{r},t)$, the boundary conditions satisfied by $g(\mathbf{r},t|\mathbf{r}',t')$ are (Appendix A)

$$g(\mathbf{r},t|\mathbf{r}',t') = 0$$

in the spatial domain $\mathbf{r} \in \partial\mathscr{A}_A$ and

$$\mathbf{n}_\perp\cdot\nabla\, g(\mathbf{r},t|\mathbf{r}',t') = 0$$

in the spatial domain $\mathbf{r} \in \partial\mathscr{A}_R$ and where $\mathbf{n}_\perp$ is the unit vector normal to $\partial\mathscr{A}$ pointing outward.

To compute the even moments of $g$, multiply (C2) by the scalar $r^{2N}$ and integrate over domain $\mathscr{A}$ in the interval of time $\mathscr{T}_{-\infty} = [-\infty,t]$. Explicit integration with respect to time can only be performed on the term that contains the time derivative of $g$:

$$\int_{\mathscr{T}-\infty} d\tau \int_{\mathscr{A}} d^2\mathbf{r}\, r^{2N}\,\frac{\partial g(\mathbf{r},\tau|\mathbf{r}',t')}{\partial\tau} = \int_{\mathscr{A}} d^2\mathbf{r}\, r^{2N}\, g(\mathbf{r},t|\mathbf{r}',t')$$

where I am allowed to change the order of integration by Fubinis' Theorem because the integrand is absolutely integrable (Royden 1968). I then have

$$\int_{\mathscr{T}\infty} d\tau \int_{\mathscr{A}} d^2\mathbf{r}\, r^{2N}\, \mathcal{L}g(\mathbf{r},\tau|\mathbf{r}',t') = r'^{2N} - \langle r^{2N}\rangle(t|\mathbf{r}',t')$$

where

$$\langle r^{2N}\rangle(t|\mathbf{r}',t') = \int_{\mathscr{A}} d^2\mathbf{r}\, r^{2N} g(\mathbf{r},t|\mathbf{r}',t')\,.$$

For the spatial integration in the l.h.s., I apply partial integration and the Divergence Theorem to those terms containing the gradient and the Laplacian of $g$. For the term containing the gradient of $g$, this results in

$$\int_{\mathscr{A}} d^2\mathbf{r}\, r^{2N}\mathbf{b}_1(\mathbf{r},t)\cdot\nabla\, g(\mathbf{r},t\,|\,\mathbf{r}',t')$$

$$= \oint_{\partial\mathscr{A}} dl\, r^{2N}\,\mathbf{n}_\perp\cdot\mathbf{b}_1(\mathbf{r},t)\, g(\mathbf{r},t\,|\,\mathbf{r}',t')$$

$$\int_{\mathscr{A}} d^2\mathbf{r}\,\nabla\cdot[r^{2N}\mathbf{b}_1(\mathbf{r},t)]\, g\,(\mathbf{r},t\,|\,\mathbf{r}',t')$$

while for the term with the Laplacian of $g$, the same procedure generates

$$\int_{\mathscr{A}} d^2\mathbf{r}\, r^{2N} b_2(\mathbf{r},t)\,\Delta\, g(\mathbf{r},t|\mathbf{r}',t') = \oint_{\partial\mathscr{A}} dl\, r^{2N}\, b_2(\mathbf{r},t)\mathbf{n}_\perp$$

$$\cdot\nabla g(\mathbf{r},t|\mathbf{r}',t') - \oint_{\partial\mathscr{A}} dl\,\mathbf{n}_\perp\cdot\nabla\,[r^{2N}\, b_2(\mathbf{r},t)]\, g(\mathbf{r},t|\mathbf{r}',t')$$

$$+\int_{\mathscr{A}} d^2\mathbf{r}\,\Delta\,[r^{2N}\, b_2(\mathbf{r},t)]\, g(\mathbf{r},t|\mathbf{r}',t')\,.$$

The boundary integrals are used to satisfy the boundary conditions. After doing so, I am left with

$$\int_{\mathscr{T}-\infty} d\tau \int_{\mathscr{A}} d^2\mathbf{r}\, E(\mathbf{r},\tau)\, g(\mathbf{r},\tau|\mathbf{r}',t') + \int_{\mathscr{T}-\infty} d\tau\, C_E(\tau|\mathbf{r}',t')$$

$$= r'^{2N} - \langle r^{2N}\rangle(t|\mathbf{r}',t')$$

where

$$E(\mathbf{r},\tau) = r^{2N}\, b_0(\mathbf{r},\tau) - \nabla \cdot [r^{2N}\, \mathbf{b}_1(\mathbf{r},\tau)] + \triangle\, [r^2 b_2(\mathbf{r},\tau)]$$

and

$$C_E(\tau|\mathbf{r}',t') = \begin{cases} -\oint_{\partial\mathcal{A}} dl\, r^{2N}\, k(\mathbf{r},t)\, \mathbf{n}_\perp \cdot \nabla\, g(\mathbf{r},\tau|\mathbf{r}',t') & \text{for } \partial\mathcal{A}_A \\ +\oint_{\partial\mathcal{A}} dl\, \mathbf{n}_\perp \cdot (\nabla r^{2N})\, k(\mathbf{r},t) g(\mathbf{r},\tau|\mathbf{r}',t') & \text{for } \partial\mathcal{A}_R\,. \end{cases}$$

Discretizing time in these expressions for a single interval of time for a source time $t_j$, I have

$$\left[\int_{\mathcal{A}} d^2\mathbf{r}\, E(\mathbf{r},t_j) g(\mathbf{r},t_j|\mathbf{r}',t_j) + C_E(t_j|\mathbf{r}',t_j)\right]$$

$$= \frac{1}{\mathcal{T}_j}\left[r'^{2N} - \langle\, r^{2N} \rangle\, (t_{j+1}|\mathbf{r}',t_j)\right]$$

where

$$\langle\, r^{2N} \rangle\, (t_{j+1}|\mathbf{r}',t_j) = \int_{\mathcal{A}} d^2\mathbf{r}\, r^{2N} g(\mathbf{r},t_{j+1}|\mathbf{r}',t_j)\,.$$

As can be appreciated, the integrals on the l.h.s. of the expression have $g(\mathbf{r},t_j|\mathbf{r}',t_j)$ in the integrand. Making use of the initial property of $g$:

$$g(\mathbf{r},t_j|\mathbf{r}',t_j) = \delta(\mathbf{r}-\mathbf{r}')\,.$$

Integrating with the reminder that $\partial\mathcal{A} \subset \mathcal{A}$, I can conclude

$$E(\mathbf{r}',t_j) = r'^{2N}\, b_0(\mathbf{r}',t_j) - \nabla' \cdot \left[r'^{2N}\, \mathbf{b}_1(\mathbf{r}',t_j)\right]$$

$$+ \nabla'\left[r'^{2N}\, \mathbf{b}_2(\mathbf{r}',t_j)\right]$$

by use of the properties of the gradient of Dirac delta functions (Lighthill 1964; Butkov 1968) and the assumption that $\partial\mathcal{A}$ is piecewise smooth:

$$C_E(\mathbf{r}',t_j) = C_E(t_j|\mathbf{r}',t_j)$$

$$= \begin{cases} 0 & \text{if } \mathbf{r}' \notin \partial\,\mathcal{A} \\ \nabla' \cdot [\boldsymbol{n}_\perp \mathbf{r}'^{2N} k(\mathbf{r}',t_j)] & \text{if } \mathbf{r}' \in \partial\,\mathcal{A}_{\mathcal{A}} \\ \boldsymbol{n}_\perp \cdot (\nabla' r'^{2N}) k(\mathbf{r}',t_j) & \text{if } \mathbf{r}' \in \partial\,\mathcal{A}_{\mathfrak{R}}\,. \end{cases}$$

Evidently, $E(\mathbf{r}',t_j)$ is correct for points in $\mathcal{A}$ regardless of the boundaries. Therefore, it is also correct for the boundless domain. Henceforth, I shall ignore the terms with the source at the boundary of the domain because data are seldomly collected there.

Using the identities

$$\nabla' \cdot \mathbf{r}' = 2\,,$$

which is a consequence of $\mathcal{A} \in \mathbf{R}^2$,

$$\nabla' \mathbf{r}'^{2N} = 2N r'^{2N-2} \mathbf{r}'\,,$$

and

$$\nabla' \cdot (r'^{2N-2} \mathbf{r}') = 2N r'^{N-2}$$

to expand $E(\mathbf{r}',t_j)$ leads to the expression

$$E(\mathbf{r}',t_j) = r'^{2N} b_0(\mathbf{r}',t_j) - 2N r'^{2N-2} [\mathbf{r}' \cdot \mathbf{b}_1(\mathbf{r}',t_j)]$$

$$- r'^{2N}\, \nabla' \cdot \mathbf{b}_1(\mathbf{r}',t_j) + 4\, N^2 r'^{2N-2} b_2[\mathbf{r}',t_j)]$$

$$+ 4\, N r'^{2N-2}\, [\mathbf{r}' \cdot \nabla' b_2(\mathbf{r}',t_j)] + r_k'^{2N}\, \triangle' b_2(\mathbf{r}',t_j)\,.$$

Discretizing space with $\mathbf{r}_k$ as the source point and $\mathbf{r}_i$ as the receiver point, and substituting for $\{b_0,\mathbf{b}_1,b_2\}$ their expressions in terms of $\{m,\mathbf{v},k\}$, yields

$$E(\mathbf{r}_k,t_j) = r_k^{2N} m(\mathbf{r}_k,t_j) - 2\, N r_k^{2N-2}\, [\mathbf{r}_k \cdot \mathbf{v}(\mathbf{r}_k,t_j)] - 4\, N^2 r_k^{2N-2} k(\mathbf{r}_k,t_j)$$

$$-2\, N r_k^{2\,N-2}\, [\mathbf{r}_k \cdot \nabla_k k(\mathbf{r}_k,t_j)]$$

where I am using the notation

$$\nabla_i k(\mathbf{r}_i,t_j) = [\nabla k(\mathbf{r},t_j)]_{\mathbf{r}=\mathbf{r}_i}\,.$$

The scalar equations for the even moments of the Green function for source points $\mathbf{r}_k \notin \partial\mathcal{A}$ are then

$$E(\mathbf{r}_k,t_j) = \frac{1}{\mathcal{T}_j}\, [r_k^{2N} - \langle\, r_i^{2N} \rangle\, (t_{j+1}|\mathbf{r}_k,t_j)]$$

and where

$$\langle\, r_i^{2N} \rangle\, (t_{j+1}|\mathbf{r}_k,t_j)] = \sum_{i=1}^{n} \mathcal{A}_i r_i^{2N}\, g(\mathbf{r}_i,t_{j+1}|\, \mathbf{r}_k,t_j)\,.$$

With these, I can generate the zeroth ($N = 0$), second ($N = 1$), . . ., moments of the Green function.

To derive the odd-moments equation, I can initially multiply the field equation for the Green function by $r^{2N}\mathbf{r}$ and perform analogous operations using the algebra and calculus of dyads. This leads to the vector $\boldsymbol{O}(\mathbf{r}_k,t_j)$ analogous to the scalar $E(\mathbf{r}_k,t_j)$ given by

$$\boldsymbol{O}(\mathbf{r}_k,t_j) = r_k^{2N}\mathbf{r}_k m(\mathbf{r}_k,t_j) - r_k^{2N}\mathbf{v}(\mathbf{r}_k,t_j) - 2\,Nr_k^{2N-2}\mathbf{r}_k\,[\mathbf{r}_k \cdot \mathbf{v}(\mathbf{r}_k,t_j)]$$

$$-4\,N(N+1)r_k^{2N-2}\mathbf{r}_k k(\mathbf{r}_k,t_j) - r_k^{2N}\,\nabla_k k(\mathbf{r}_k,t_j)$$

$$-\,2\,Nr_k^{2N-2}\mathbf{r}_k\,[\mathbf{r}_k \cdot \nabla_k k(\mathbf{r}_k,t_j)]$$

for $\mathbf{r}_k \notin \partial\mathcal{A}$. The vector equations for the odd moments of the Green function are then

$$\boldsymbol{O}(\mathbf{r}_k,t_j) = \frac{1}{\mathcal{T}_j}\,[r_k^{2N}\mathbf{r}_k - \langle\, r_i^{2N}\mathbf{r}_i \,\rangle\,(t_{j+1}|\mathbf{r}_k,t_j)]$$

where

$$\langle\, r_i^{2N}\mathbf{r}_i \,\rangle\,(t_{j+1}|\mathbf{r}_k,t_j) = \sum_{i=1}^{n}\,\mathcal{A}r_i^{2N}\mathbf{r}_i g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_j)\,.$$

With these; I can generate the first $(N = 0)$ , third $(N = 1)$, . . ., moments of the Green function.

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# DETECTING THE ECOLOGICAL EFFECTS OF ENVIRONMENTAL IMPACTS: A CASE STUDY OF KELP FOREST INVERTEBRATES[1]

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*Abstract.* Detecting the environmental impacts of human activities on natural communities is a central problem in applied ecology. It is a difficult problem because one must separate human perturbations from the considerable natural temporal variability displayed by most populations. In addition, most human perturbations are generally unique and thus unreplicated. This raises the problem of deciding whether observed local effects are due to human intervention or to the natural differences in temporal patterns that often occur among different sites. These problems can be successfully addressed with the Before–After/Control–Impact (BACI) sampling design, in which Impact and Control sites are sampled contemporaneously and repeatedly in periods Before and After the human perturbation of interest. In the present case, we use this design to examine the ecological effects of the cooling water discharge from a coastal nuclear power plant in southern California.

The results suggest some general lessons about the process of impact assessments that are applicable in many ecological contexts. In systems where plants and animals are long-lived and recruit sporadically, the rates of change in density are often so low that sampling more than a few times per year will introduce serial correlations in the data. As a result, for studies of few years duration, few samples will be taken. A small sample size means that the tests of the assumptions underlying the statistical analyses, e.g., independence and additivity, will have low power. This injects uncertainty into the conclusions. Small sample size also means that the power to detect any but very large effects will be low. In our study, sampling periods of 2–3 yr both Before and After the impact were not long enough to detect a halving or doubling of populations at the impact site. We concluded that there were significant environmental impacts because: (1) the effect size was generally very large ($\approx -75\%$); (2) there was a consistent pattern among species; (3) there were two Impact sites, and effects were larger at the site nearest the discharge; (4) the observed effects accorded with physical changes that could be linked with the source of impact; and (5) a number of alternative mechanisms, unrelated to the source of impact, were examined and rejected.

Relative to control populations, there were statistically significant reductions in density of snails, sea urchins, and sea stars, all of which occurred primarily on rocky substrates. All of the reductions were larger at the Impact station about 0.4 km from the discharge than at a second Impact station 1.4 km away. The most plausible mechanisms for the declines seem to be linked to the turbidity plume created by the power plant and the resultant increase in suspended inorganic and organic materials (+46% at the Impact site nearest the discharge). Any associated flux of fine particles on rocks would have deleterious effects on many of the hard benthos. Populations of two filter-feeding species, a gorgonian coral and a sponge, showed relative increases in density. Although the increase in populations of filter feeders could be related to the ingestion, killing, and discharge of tons of plankton by the cooling system, an alternative natural mechanism was also considered reasonable.

Monitoring studies of relatively long-lived organisms will often have low power to detect ecologically significant changes in density. The present study of kelp forest organisms extended over nearly 6 yr, yet the resulting statistical tests generally had power of <30% to detect a doubling or halving in density at a significance level of .05. In such a community it would be a mistake to conclude that there were no significant ecological effects based on conventional hypothesis tests. Unless there is a willingness to accept the fact that changes in natural populations on the order of 50% will often go undetected, the standards and types of evidence used to demonstrate environmental impacts must be changed.

*Key words: BACI statistical analysis; California; effect size; effluent; environmental impact assessment; kelp forest invertebrates; nuclear power plants; open coast; pollution; serial correlation; statistical power; turbidity.*

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## INTRODUCTION

A central problem in applied ecology is the detection of the impacts of human activities on natural communities. Since abundance and other attributes of most natural populations vary greatly in space and time, the detection of anthropogenic perturbations against the background of the naturally occurring variation poses non-trivial methodological and statistical problems (Hurlbert 1984). However, recent work has shown that these problems are potentially tractable (Eberhardt 1976, Skalski and McKenzie 1982, Stewart-Oaten et al. 1986, Carpenter 1989, Carpenter et al. 1989, Underwood 1991, Stewart-Oaten et al. 1992). There is an emerging consensus that in order to detect impacts one should sample repeatedly and contemporaneously at the potential impact site, and at one or more control sites during the periods before and after the impact has begun.

Stewart-Oaten et al. (1986) suggest that to judge whether an impact has occurred one calculate the differences in the variate of interest, generally abundance, between the Impact and Control sites on each survey and compare the averages of these differences in the Before and After periods. The critical elements in this design are that the populations at the Control and Impact sites be sampled at about the same time during each survey and that they vary in about the same way, or track one another, prior to the perturbation being studied. The two populations do not have to have equal densities and their densities do not have to be constant. There may be natural secular trends, cycles, or seemingly non-periodic fluctuations in the populations, but if the populations track one another, the differences between the two sites will vary randomly about some mean value in the Before period. If there is an effect of the perturbation on the mean population at the Impact site, the average difference between it and the Control population will increase or decrease. Provided that certain statistical criteria are satisfied, a statistically significant change in the average difference, or "delta," between the populations after the onset of the perturbation is strong evidence of an ecological effect of the environmental impact. This sampling design is called the Before–After/Control–Impact design (BACI).

From 1980 to 1987 we conducted studies of the ecological effects of the cooling water discharge from two new generating units of the San Onofre Nuclear Generating Station, which is located on the open coast in northern San Diego County, California. Here we present the results of studies of the impacts of the discharge on invertebrates that inhabit forests of giant kelp, *Macrocystis pyrifera*. We used the BACI sampling design, with a few modifications, to detect effects on population densities. We tested for changes from before to after the new generating units began operating, estimated the size of these effects, and calculated the power of the tests. One modification of the BACI design was the incorporation of a second impact site into the analysis. The intent of having two impact sites located at different distances from the generating station was to provide some information on the size of the area affected.

Other investigators were engaged in assessing the effects of the power plant on the physical environment, and a great deal of oceanographic data were collected during the period of our studies. We have examined these data for physical correlates to the biological changes we observed, which provide clues to the mechanisms underlying the ecological effects. Comparison of oceanographic data from the Control and Impact sites also enables one to test whether large-scale changes, such as the 1982–1984 El Niño, affected the two sites differently.

The organisms we studied are long-lived and recruit infrequently. These characteristics are typical for species in many communities and pose special problems for the environmental biologist. This study has taught us some lessons that we think may be germane in many ecological contexts.

## METHODS

### *San Onofre Nuclear Generating Station*

The San Onofre Nuclear Generating Station consists of three units. Unit 1 was commissioned in 1968. Units 2 and 3, the subjects of our study, began operating near their full combined capacity in 1983. Each of the new units contains a pressurized-water nuclear reactor with an electrical output of 1100 MW. The steam used to drive the turbines is generated by heat from the reactor and is then cooled by exchanging heat with ambient sea water.

The once-through cooling system for each unit has a maximum flow rate of 3137 $m^3$/min ($1.66 \times 10^6$ gal/min) and raises the temperature of the withdrawn sea water 10.7°C (MRC 1988*a*). The intake structures of both units are located 970 m offshore in 9.1 m of water (Fig. 1) and withdraw water from ≈2.1 m above the sea floor. After passing through the cooling system of the power plant, the heated water is directed offshore where it is discharged through two diffuser pipes. Each diffuser pipe is ≈800 m long and perpendicular to the shoreline. The diffuser structures for Unit 2 lie seaward of the structures for Unit 3, so that together, the diffusers extend from ≈1.0 km to 2.5 km offshore from the power plant. Along each pipe the heated water is discharged through diffuser ports located in 63 evenly spaced outfall riser. The openings of the diffuser ports are ≈2.2 m above the sea floor, are ≈0.6 m in diameter, and are angled upwards and alternately upcoast and downcoast.

The diffuser system was designed to discharge the heated effluent without increasing local sea-surface temperatures above regulatory thermal standards.

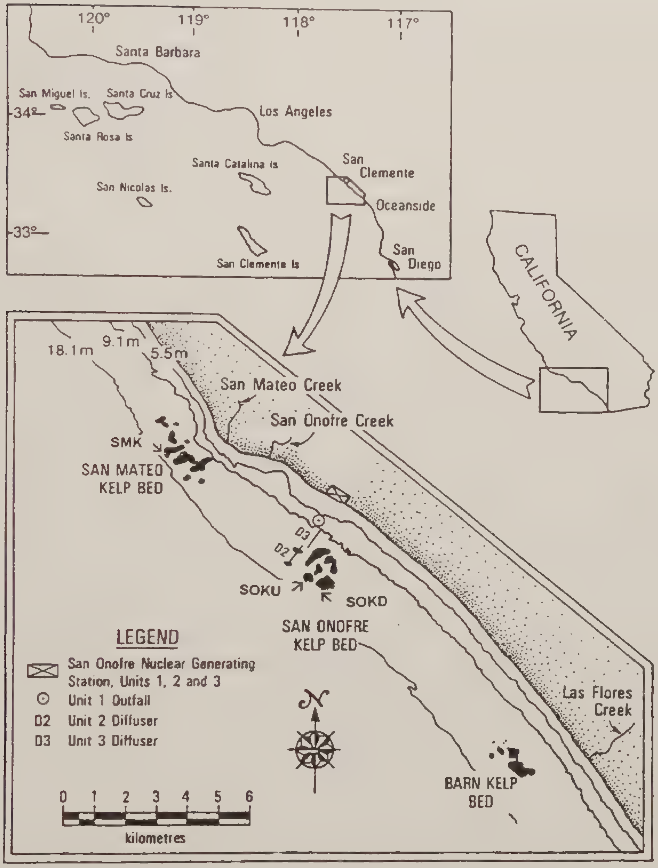
120°
119°
118°
117°
Santa Barbara
San Miguel Is.
Santa Cruz Is
34°
Santa Rosa Is
Los Angeles
Santa Catalina Is
San Clemente
San Nicolas Is.
Oceanside
33°
San Clemente Is
San Diego
CALIFORNIA
18.1m
9.1m
5.5m
San Mateo Creek
San Onofre Creek
SMK
SAN MATEO KELP BED
D3
D2
SOKU
SOKD
SAN ONOFRE KELP BED
LEGEND
San Onofre Nuclear Generating Station, Units 1, 2 and 3
Unit 1 Outfall
D2 Unit 2 Diffuser
D3 Unit 3 Diffuser
0 1 2 3 4 5 6
kilometres
N
Las Flores Creek
BARN KELP BED

FIG. 1. San Onofre Region. SOKU is the Near Impact site, SOKD is the Far Impact site, and SMK is the Control site.

Rapid cooling is effected because the 63 discharge jets entrain and turbulently mix with ambient water. The volume of entrained water is ≈10 times that of the discharged water. A major consequence of the cooling system design is that the discharge adds a large flux of seaward momentum to local waters (Eco-M 1988). The large and rapid upward and seaward redirection of water and associated suspended inorganic particles and passive organisms appears to be one of the two most significant impacts of Units 2 and 3 on the local physical environment. A second similar impact results from withdrawing turbid nearshore water and discharging it offshore. The cooling water effluent is discharged ≈0.4 km upcoast (northwest) of the San Onofre kelp forest (Fig. 1).

### *Study sites*

Two stations were established in the San Onofre kelp forest, the site of potential impacts on kelp forest organisms. Both were at a depth of ≈14.5 m. The Near Impact site (Fig. 1: SOKU) was placed as near to the diffusers as possible within the kelp forest, ≈400 m downcoast. The Far Impact site (Fig. 1: SOKD) was placed as far from the diffusers as possible within the kelp forest, ≈1400 m downcoast. This design allowed us to determine whether effects were detectable throughout the kelp forest or were confined to some area closer to the diffusers than the Far Impact station. A third site, the Control (Fig. 1: SMK) was located in the San Mateo kelp forest, 4.5 km to the northwest in ≈12.5 m of water. All of the study sites remained inside of kelp forest boundaries for the duration of the study.

Each site consisted of a metal plate that marked the origin of four 40 m long transects. The transects were oriented in the shape of a cross. Steel rods were driven into the substrate every metre along the transects to help divers find their way during the frequent periods of poor visibility. A permanent 1-m$^2$ quadrat was positioned every 4 m along each transect. Thus, at each study site, there were 40 fixed quadrats within which plants and animals were periodically censused. All the sites were located under kelp canopy and placed so that each of the permanent quadrats was at least 10 m from the nearest sand patch.

### *Species studied*

The invertebrate species studied were chosen because they are common members of kelp forest communities in southern California and are easily and reliably counted by divers in the field, even under conditions of poor underwater visibility. Thus, while a number of larger motile and sessile invertebrate species were sampled, most sessile species, including the smaller species that make up the "fouling" community on many rocky substrates (e.g., bryozoans, hydroids, and most sponges), were not. Forty-one species of invertebrates were counted (Table 1). Twenty-three species were sampled from the beginning of the study. Five species of snails were added to the sample list during the first few surveys, and an additional 13 species of snails were added beginning with the penultimate Before sample.

Of the 41 species sampled, 22 were rare throughout the study. Most of these were absent from two of the three study sites throughout the After period. Two were absent at the Control throughout the Before period and during most of the After period. Data for these species were not analyzed. Red sea urchins, *Strongylocentrotus franciscanus*, were sampled, but the data were not analyzed because differential effects of harvesting could be confounded with a power plant effect. Throughout the Before period red urchins were commercially harvested in both kelp forests. By late 1984 there were so few red urchins left in the San Onofre kelp forest that commercial harvesting was no longer feasible. However, harvesting continued at San Mateo. We've considered the possibility that reductions of red urchin populations from harvesting may have indirectly affected the abundances of other species. No experiments were done to test this hypothesis. However, since harvesting tended to bring red urchin populations to similar low numbers at our sampling stations at both Control and Impact sites, we think it unlikely that it would bias our estimates of a potential power plant effect.

Beginning on the fourth survey in the After period, a large feeding aggregation, or "front," of red sea urchins moved onto parts of the Control site in the San Mateo kelp forest. By the end of the study this front had occupied all of the quadrats on two of the four transects. There are well-documented cases of such fronts adversely affecting both algal (Dean et al. 1984) and invertebrate (Ebert 1977; S. C. Schroeter, J. D. Dixon, and R. O. Smith, *personal observations*) communities. Therefore, data from the quadrats occupied by the front were not included in the analyses. As a result, means at the Control site had sample sizes for the last five surveys of 39, 34, 31, 27, and 20, rather than 40.

The data for the remaining 18 species were examined for effects of the power plant on density (Table 1). The data for 14 of these species were suitable for the *t* test using the Near Impact station (Tables 3 and 4), and 10 species passed the more restrictive screen for the analysis of variance using both impact stations (Table 5).

### *Plant operating schedule and sampling methods*

By May 1983 Units 2 and 3 were circulating water at rates near the projected long-term operating levels (Fig. 2). For our analyses, we considered the period from November 1980 to the end of April 1983 to be the preoperational or Before period, during which 10 surveys were conducted at 2–4 mo intervals. Since the species we studied are long-lived and recruit sporadically, we thought there should be a time lag between the Before and After periods. Accordingly, a 16-mo interim period from May 1983 to the beginning of October 1984 elapsed before operational, or "After," samples were taken. During the interim period, surveys were conducted semiannually. The After period extended from early October 1984 through December 1986, during which eight quarterly surveys were conducted.

The time and effort required to complete a survey varied substantially, depending on sea conditions, visibility, and the abundance of organisms. The time elapsed from the first to the last sample during a survey varied from 5 d to 33 d, and sampling effort varied from 16 to 32 diver-days. Surveys usually included a training day when all divers would sample the same quadrats under the supervision of the field leader.

To avoid disturbing sessile species, only those animals on exposed surfaces were counted. Cracks and crevices and the sides of rocks were examined, but boulders and cobbles were not overturned. Species such as sea urchins, sea stars, and snails, which could quickly move out of the quadrat, were counted first. Individuals moving into a quadrat after counting began were not counted.

The distribution of substrate types was also estimated. Within each quadrat, the substrate under each of 15 uniformly distributed points was noted as sand and gravel (diameter <1 cm), cobble (1–30 cm), boulder (>30 cm), or bedrock reef. The longest dimension of cobbles and boulders was measured to the nearest centimetre. Mud was added as a substrate type when it was first observed in the San Onofre kelp forest in October 1985.

Temperature, underwater irradiance, and seston flux were measured near each of our stations by Eco-Systems Management Associates using underwater instrument systems of their own design (Eco-M 1987). Temperature sensors were deployed at the surface and near

TABLE 1. Species of large kelp forest invertebrates used to test for an effect of the cooling water discharge of the San Onofre (California) nuclear power plant. "Before" and "after" refer to the periods of time before and after full power operation of the plant began.

| Species* | Number of surveys | | Statistical analyses performed? | | |
|---|---|---|---|---|---|
| | Before | After | Assump.† | *t* test | ANOVA |
| Porifera | | | | | |
| *Tethya aurantia* | 10 | 8 | Yes | Yes | No |
| Cnidaria | | | | | |
| *Lophogorgia chilensis* (R) | 10 | 8 | No | No | No |
| *Muricea californica* | 10 | 8 | Yes | Yes | No |
| *Muricea fruticosa* (A) | 10 | 8 | Yes | No | No |
| *Pachycerianthus fimbriatus* (R) | 10 | 8 | No | No | No |
| Annelida | | | | | |
| *Diopatra ornata* (R) | 10 | 8 | No | No | No |
| Mollusca | | | | | |
| *Astraea undosa* (T) | 7 | 8 | Yes | No | No |
| *Calliostoma* spp. (R) | 2 | 5 | No | No | No |
| *Conus californicus* | 6 | 8 | Yes | Yes | Yes |
| *Crassispira semiinflata* (T) | 5 | 5 | Yes | No | No |
| *Cypraea spadicea* | 9 | 8 | Yes | Yes | No |
| *Haliotis corrugata* (R) | 10 | 8 | No | No | No |
| *Haliotis rufescens* (R) | 10 | 8 | No | No | No |
| *Hesperato vitellina* (R) | 2 | 8 | No | No | No |
| *Kelletia kelletii* | 10 | 8 | Yes | Yes | Yes |
| *Latiaxis oldroydi* (R) | 2 | 8 | No | No | No |
| *Maxwellia gemma* | 2 | 8 | Yes | Yes | Yes |
| *Mitra idae* | 6 | 8 | Yes | Yes | Yes |
| *Murexiella santarosana* | 2 | 7 | Yes | Yes | Yes |
| *Nassarius* spp. | 2 | 7 | Yes | Yes | No |
| *Ophiodermella inermis* (R) | 2 | 5 | No | No | No |
| *Pteropurpura festiva* | 2 | 8 | Yes | Yes | Yes |
| *Pteropurpura vokesae* (R) | 2 | 8 | No | No | No |
| *Tegula aureotincta* | 2 | 5 | Yes | Yes | No |
| *Tegula eiseni* (R) | 2 | 8 | No | No | No |
| *Trivia solandri* (R) | 2 | 8 | No | No | No |
| *Trivia californica* (R) | 2 | 8 | No | No | No |
| Echinodermata | | | | | |
| Sea Urchins | | | | | |
| *Centrostephanus coronatus* (R) | 10 | 8 | No | No | No |
| *Lytechinus anamesus* (SC) | 10 | 8 | Yes | Yes | Yes |
| *Strongylocentrotus purpuratus* | 10 | 8 | Yes | Yes | Yes |
| *Strongylocentrotus franciscanus* (C) | 10 | 8 | No | No | No |
| Sea Stars | | | | | |
| *Asterina (= Patiria) miniata* | 10 | 8 | Yes | Yes | Yes |
| *Astrometis sertulifera* (R) | 10 | 8 | No | No | No |
| *Dermasterias imbricata* (R) | 10 | 8 | No | No | No |
| *Henricia leviuscula* (R) | 10 | 8 | No | No | No |
| *Linckia columbiae* (R) | 10 | 8 | No | No | No |
| *Orthasterias koehleri* (R) | 10 | 8 | No | No | No |
| *Pisaster giganteus* (R) | 10 | 8 | No | No | No |
| *Pisaster brevispinnus* (R) | 10 | 8 | No | No | No |
| Sea Cucumber | | | | | |
| *Parastichopus parvimensis* (R) | 10 | 8 | No | No | No |
| Urochordata | | | | | |
| *Styela montereyensis* (SC, T) | 10 | 8 | Yes | No | No |

* R = too rare to analyze; A = deltas (differences between population densities at Impact and Control sites on each survey) are non-additive in the Before period; T = linear trend in the deltas in the Before period; SC = deltas are serially correlated in the Before period; C = commercially harvested.

† Assump. = tests for assumptions.

the bottom. Temperature was recorded every hour in digital loggers (PROM, a Programmable Read Only Memory Semi-conductor chip [Intel Corporation, Santa Clara, California, USA]). Underwater irradiance was measured within the 400–700 nm wavelength range with LI-COR LI-192S Underwater Quantum Sensors. Integrated irradiance values were recorded every hour in digital loggers (PROM). The PROMs were read every

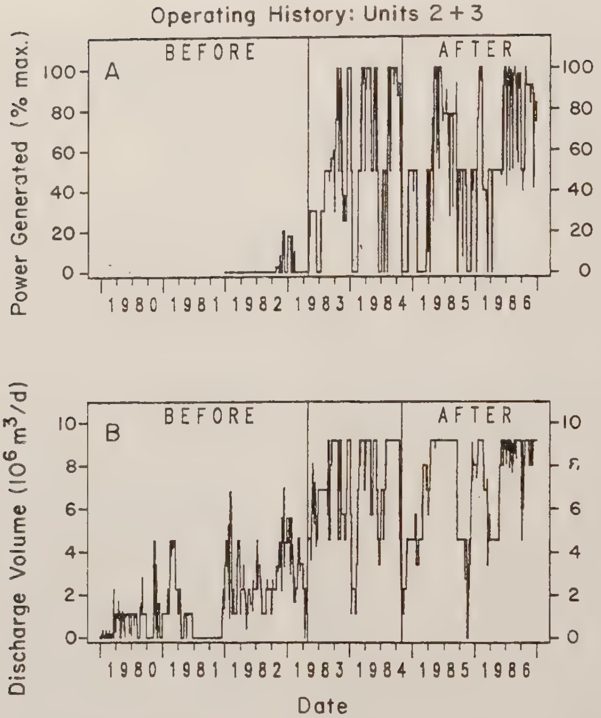

FIG. 2. Combined operating history of Units 2 and 3 of the San Onofre Nuclear Generating Station. The effluent is heated significantly above ambient temperature only when power is being generated. From 1980 to 1983 the new generating units were undergoing testing.

2–3 wk and the data transferred to computer files (Eco-M 1987).

Seston flux was estimated by measuring the accumulation of sediment within sediment traps. The traps were acrylic tubes 2.5 cm in diameter and 30 cm long, closed at the bottom with a rubber stopper. Sets of three tubes were held vertically in the water column on floating racks 2 m above the bottom at each sampling site. The traps were replaced approximately biweekly and the height of the accumulated sediment was measured in the laboratory. The mean of the three tubes was used as the variate in the analysis (Eco-M 1987).

### *Statistical design and analysis*

We did two types of analyses based on the Before–After/Control–Impact (BACI) sampling design (Stewart-Oaten et al. 1986) to test for the presence of a power plant effect: the *t* test and the analysis of variance. We estimated the density of organisms at about the same time at Control and Impact sites on replicate surveys during ≈2.5-yr periods Before and After the power plant began operation. To test for an effect of the power plant we first log-transformed the data to achieve additivity (Stewart-Oaten et al. 1986). We then calculated the differences (deltas) between the values at the Impact and Control sites on each survey.

*t test.*—Deltas were averaged over each operational period. The difference between the average Before and After deltas provides an estimate of the effect of the power plant on density. A *t* test was done to determine whether this difference was significantly different ($P \leq .05$) from zero. Before log transformation, the model underlying the *t* test (Table 2) can be represented as:

$$X_{ijk} = mS_{i(j)}P_jL_kE\epsilon_{ijk}, \qquad (1)$$

where $X$ is abundance at the $i$th survey, in the $j$th operational period, and the $k$th location; $m$ = the mean value at the Control site during the Before period, $S_{i(j)}$ = the effect of Survey $i$ in Period $j$; $L_k$ = the effect of Location: $L_1 = 0$ (Control), $L_2 = I$ (Impact); $P_j$ = the effect of operational period: $P_1 = 0$ (Before period), $P_2 = A$ (After period); $E$ = the effect of the impact: $E = e$ at the Impact site in the After period and 0 otherwise; and $\epsilon_{ijk}$ = error.

We assume that $\log(\epsilon_{ijk})$ is normal, with mean = 0,

TABLE 2. Expected values for the BACI statistical model. Symbols are explained in *Methods: Statistical design and analysis: t test*.

| Survey | Expected value at Control | Expected value at Impact | Expected Impact − Control (delta) |
|---|---|---|---|
| Survey $i$, during the Before period | $\log(m) + \log(S_{i(j)})$ | $\log(m) + \log(S_i) + \log(I)$ | $\log(I)$ |
| Survey $j$, during the After period | $\log(m) + \log(S_j) + \log(A)$ | $\log(m) + \log(S_j) + \log(I) + \log(A) + \log(e)$ | $\log(I) + \log(e)$ |

We assume that $\log(\epsilon_{ijk})$ is normal with mean = 0, and log-transformation (with a constant added in the case of zero values) yields the tabled expected values for surveys in the Before and After periods.

and log-transformation (with a constant added in the case of zero values) yields the expected values for surveys in the Before and After periods that are shown in Table 2.

The estimated effect of the power plant is the difference between the mean Before and After deltas, which is an estimate of $\log(e)$. $e$ is the proportional change in the average abundance at the Impact site during the After period due to the operation of the power plant, and $(e - 1) \times 100$ is the percentage change.

Several assumptions underlie this model:

1) The data are additive. The effects of location, period, and impact are constant and can be added to the underlying mean abundance to get the expected abundances in the different cells in the design. Moreover, the temporal effects associated with individual surveys are the same at the Control and Impact sites.

2) The random errors of the deltas are independent.

3) The random errors are normally distributed with equal variances and means of zero.

Non-additivity can reduce the power to detect an effect or result in a biased estimate of an effect (Stewart-Oaten et al. 1986). If the model underlying the *t* test is the correct one, log transformation should produce an additive model. We tested this by regressing the Before deltas against the sum of the transformed Control and Impact values. This is Tukey's (1949) one-degree-of-freedom additivity test. A slope significantly different from zero indicates non-additivity.

Not all non-additivity can be dealt with by transformation. Of special concern is the case when the deltas trend positively or negatively with time in the Before period. Such trends could not be caused by the power plant, but if they continued into the After period, would confound the estimates of the effect of the power plant. We tested for trends in the deltas in the Before period by regressing them against time. If we detected a significant trend, the data were excluded from further analysis.

Lack of independence in random errors occurs if the differences between replicate deltas vary as a function of time between samples, and results in serial correlations of errors. We expect that when violations of the independence assumption occurs, this will often lead to errors close in time tending to be similar. Such positive serial correlation has the effect of underestimating the true variance of the deltas and leads to overly sensitive hypothesis tests. Durbin-Watson tests were used to detect serial correlations in the errors. This occurred once, and we replaced the standard *t* test with a time series intervention (autoregressive) model (Box and Tiao 1965, 1975, Box and Jenkins 1976, McDowall et al. 1980) using the Statistical Analysis System Proc Autoreg (Brocklebank and Dickey 1984).

Finally, the *t* test of the difference between the Before and After deltas assumes that errors are normally distributed and have equal variances. Unless they are very extreme, violations of normality have little effect on the results of the *t* test (Stewart-Oaten et al. 1992), and this assumption was not tested. Non-equality of variances can affect the *t* test when sample sizes differ. When variances between the Before and After periods differed significantly ($P \leq .05$), a Welsh–Aspin test, which corrects for inequality of variances, was used in place of the standard *t* test.

Since there were sometimes zero values, the log transformation required adding a constant. Our first choice was 0.025, the smallest possible non-zero value for mean abundance at a site (i.e., 1 individual/40 $m^2$). If the transformation with 0.025 did not produce tractable data, we tried progressively larger constants. We used the smallest constant that produced data that were additive and showed no evidence of trends during the Before period. If the assumption of additivity for the Before period could not be met, we used 0.025 as a constant for purposes of graphical presentation and for calculating relative percentage of change, but no hypothesis testing was done. For five species of snails that were abundant enough to pass the initial screening, data were collected on only two surveys during the Before period, and the additivity test could not be performed.

A separate *t* test comparing the Near Impact and Control sites was done to estimate the affects on density of the influx of mud at the Near Impact site that began in summer 1985 and buried some of the fixed quadrats. For this analysis we used only those quadrats that were entirely free of mud during every survey. There were 26 quadrats that fulfilled this criterion. We did not

TABLE 3. Back-transformed average densities by Period (Before vs. After the start of full power operation of the San Onofre [California] nuclear power generating plant) for large kelp forest invertebrates at the Near (SOKU) and Far (SOKD) Impact sites (near the plant's cooling-water discharge), and the Control (SMK).

| Species | Near Impact | | Far Impact | | Control | |
|---|---|---|---|---|---|---|
| | Before | After | Before | After | Before | After |
| | Densities (individuals/m$^2$) | | | | | |
| Porifera | | | | | | |
| *Tethya aurantia* | 0.15 | 0.10 | 0.05 | 0.05 | 0.07 | 0.03 |
| Cnidaria | | | | | | |
| *Muricea californica* | 0.20 | 1.53 | 0.24 | 5.29 | 5.07 | 7.17 |
| Mollusca | | | | | | |
| *Conus californicus* | 4.43 | 1.14 | 2.93 | 1.69 | 0.69 | 1.77 |
| *Cypraea spadicea* | 0.11 | 0.08 | 0.06 | 0.05 | 0.10 | 0.21 |
| *Kelletia kelletii* | 2.90 | 1.02 | 2.92 | 1.47 | 2.52 | 2.35 |
| *Maxwellia gemma* | 0.78 | 0.12 | 0.22 | 0.14 | 0.25 | 0.41 |
| *Mitra idae* | 0.76 | 0.77 | 0.34 | 0.80 | 0.07 | 0.22 |
| *Murexiella santarosana* | 0.42 | 0.11 | 0.20 | 0.07 | 0.42 | 0.44 |
| *Nassarius* spp. | 0.36 | 0.26 | 0.75 | 0.52 | 0.22 | 0.24 |
| *Pteropurpura festiva* | 2.98 | 0.83 | 4.29 | 1.33 | 0.50 | 1.08 |
| *Tegula aureotincta* | 0.19 | 0.04 | 0.02 | 0.06 | 0.02 | 0.10 |
| Echinodermata | | | | | | |
| Sea Urchins | | | | | | |
| *Lytechinus anamesus* | 9.35 | 16.61 | 8.89 | 35.90 | 1.44 | 13.31 |
| *Strongylocentrotus purpuratus* | 0.16 | 0.11 | 0.08 | 0.08 | 1.40 | 1.03 |
| Sea Stars | | | | | | |
| *Asterina* (= *Patiria*) *miniata* | 1.14 | 0.11 | 0.52 | 0.29 | 0.09 | 0.07 |

include the last two After surveys because only a few quadrats (12 and 6) were free of mud.

We also did $t$ tests on seston flux and irradiance. One of the most obvious of the physical effects of the operation of the power plant was the frequent creation of a turbidity plume by the discharge from the diffusers. Whenever present, this plume was carried over the San Onofre kelp forest if the long shore currents were flowing to the south, which they did ≈60% of the time (MRC 1989*a*). We expected this plume to decrease the amount of underwater irradiance and increase the flux of seston near the sea floor in the San Onofre kelp forest relative to the Control, the San Mateo kelp forest. We did not expect water temperature near the bottom to be affected by the power plant. However, temperature was useful for assessing the similarity of the physical environments at the Control and Impact sites, especially during the 1982–1984 El Niño.

*Analysis of variance.*—The $t$ test was done to test for the effect of the power plant on the Near Impact site. The fact that we also sampled at a Far Impact site allowed us to do an additional analysis to determine whether the significance and size of the impact varied with distance from the power plant's diffuser discharge. Rather than $t$ tests described by Stewart-Oaten et al. (1986), we used an analysis of variance to compare simultaneously the two sets of deltas: Near Impact − Control and Far Impact − Control. The model for this design is:

$$d_{ijk} = m + P_i + L_j + PL_{ij} + S_{k(i)} + \epsilon_{ijk}, \qquad (2)$$

where $d_{ijk}$ = the difference between the Near or Far Impact and the Control values (log-transformed as before) on a given date; $m$ = the underlying mean difference in abundance; $P_i$ = the effect of the $i$th Period (Before or After); $L_j$ = the effect of the $j$th Location (Near or Far Impact); $PL_{ij}$ = the Period × Location interaction; $S_{k(i)}$ = the effect of the $k$th Survey within the $i$th Period; and $\epsilon_{ijk}$ is random error.

Period, Location, and Survey are the main effects in the model. A significant Period effect indicates that the power plant has affected abundances averaged over both of the Impact sites. A significant Period × Location interaction indicates that the power plant affected the two impact sites differently. The Location effect measures differences in the average deltas independent of any power plant effect. Since this doesn't inform us about the plant's effect, we did not report on its significance. The tests are valid even if errors for the Near and Far Impact sites are correlated. The analysis of variance is equivalent to univariate $t$ tests for differences between periods. The Period effect is equivalent to a $t$ test of the difference from Before to After in the average of two deltas: Control − Near Impact, and Control − Far Impact. The Period × Location interaction is equivalent to a $t$ test using the differences

TABLE 4. Results of $t$ tests comparing the average difference in density of large kelp forest invertebrates at the Near Impact and Control sites during the periods Before and After the start of full-power operation of the nuclear power plant. $P$ values ≤ .05 are in bold.

| Species | Number of surveys | | $P$ value | Effect size (%) | Power (%) |
|---|---|---|---|---|---|
| | Before | After | | | |
| Porifera | | | | | |
| *Tethya aurantia* | 10 | 8 | .966 | + 16.9 | 72.5 |
| Cnidaria | | | | | |
| *Muricea californica* | 10 | 8 | <**.001** | + 318.0 | 46.0 |
| Mollusca | | | | | |
| *Conus californicus* | 6 | 8 | <**.002** | −90.8 | 64.7 |
| *Cypraea spadicea* | 9 | 8 | **.003** | −61.9 | 39.9 |
| *Kelletia kelletii* | 10 | 8 | <**.001** | −63.5 | 72.0 |
| *Maxwellia gemma* | 2 | 8 | **.019** | −88.9 | 11.9 |
| *Mitra idae* | 6 | 8 | .151 | −70.6 | 11.2 |
| *Murexiella santarosana* | 2 | 7 | **.009** | −86.3 | 16.3 |
| *Nassarius* spp. | 2 | 7 | .476 | −36.3 | 10.1 |
| *Pteropurpura festiva* | 2 | 8 | .111 | −84.2 | 8.5 |
| *Tegula aureotincta* | 2 | 5 | **.013** | −93.2 | 9.1 |
| Echinodermata | | | | | |
| Sea Urchins | | | | | |
| *Lytechinus anamesus*[ar] | 10 | 8 | **.018** | −76.6 | 43.2 |
| *Strongylocentrotus purpuratus* | 10 | 8 | .651 | +0.7 | 19.3 |
| Sea Stars | | | | | |
| *Asterina (= Patiria) miniata* | 10 | 8 | <**.001** | −85.8 | 38.1 |

[ar] = Analysis was done with first-order autoregressive model to correct for serial correlation, but power was calculated from ordinary least-squares model and overestimates true power.

between the Near and Far Impact sites as the variate. Because the $d_{ijk}$s are computed by subtracting the same control value from each of the impact values on the same survey, they are likely to be correlated. This does not affect the $F$ test provided the correlation does not vary over time (Greenhouse and Geisser 1959).

Tests for additivity, trends, and serial correlations were done on the deltas for both the Near and Far Impact sites in the Before period. The analysis of variance was done only if a common transformation produced additivity and lack of trends for both sets of deltas. In cases where these criteria were not satisfied an analysis of variance was not performed.

*Statistical significance and power.*—In our hypothesis tests, we set the significance level ($\alpha$) of the $t$ test at .05. The value of .05 is a common and arbitrarily set probability of falsely finding a difference between means when there is none (Type I error). One would also like to know the probability of falsely concluding that there is no difference when one exists. This Type II error (usually designated as $\beta$) depends on the variability of the data, the number of samples taken, and the size of the difference in means one wishes to detect. Power = $1 - \beta$, and is the probability of finding a difference of a given size if it does in fact exist. In our studies, we have calculated the power to detect a halving or doubling of density with $\alpha = .05$ for the $t$ test, and for the Period effect and the Period × Site interaction in the analysis of variance.

## RESULTS

Eighteen species of kelp forest invertebrates were screened for testing for an effect of the power plant (Tables 1 and 3–5). We performed $t$ tests for nine species for which the data appeared to be additive and showed no evidence of temporal trends in the Before period, and also on the five species that were sampled only twice in the Before period and for which the data could not be tested for violations of assumptions (Table 4). The data for seven species passed the more restrictive assumption tests for the analysis of variance (Table 5). Analysis of variance was also performed on three species that were only sampled twice in the Before period.

Most of the species studied showed marked declines in population density in the impact area relative to the control area after Units 2 and 3 began operating at their normal, sustainable level. Of these, most declined in absolute numbers at the impact sites, and the declines were most pronounced nearest the diffusers (Table 3). Although not every individual result is statistically significant, the consistency of the overall pattern is notable.

### *Snails*

The majority of the species of snails that were counted declined in density in the San Onofre kelp forest during the operational, or After, period. At the same time, these species either declined to a lesser degree,

TABLE 5. Results of analysis of variance on the average difference in density of large kelp forest invertebrates at the Near Impact and Far Impact sites during the Before and After periods. The analysis simultaneously compares the Near (SOKU) and Far (SOKD) Impact sites to the Control. *P* values < .05 are in bold.

| | Effect size (%) | | Period | | | Period × Site | | |
|---|---|---|---|---|---|---|---|---|
| Species | SOKU | SOKD | *F*(df) | *P* | Power (%) | *F*(df) | *P* | Power (%) |
| Porifera | | | | | | | | |
| *Tethya aurantia* | 16.9 | 85.1 | 5.04 (1,16) | **.04** | 37.9 | 4.99 (1,16) | **.04** | 39.3 |
| Cnidaria | | | | | | | | |
| *Muricea californica* | 318.0 | 590.6[^] | ... | ... | ... | ... | ... | ... |
| Mollusca | | | | | | | | |
| *Conus californicus* | −90.8 | −81.0 | 46.46 (1,12) | **.0001** | 57.9 | 4.26 (1,12) | .06 | 50.1 |
| *Kelletia kelletii* | −63.5 | −51.8 | 12.33 (1,16) | **.003** | 77.2 | 3.12 (1,16) | .096 | 98.0 |
| *Maxwellia gemma** | −88.9 | −61.1 | 4.00 (1,8) | .08 | 16.4 | 6.00 (1,8) | **.04** | 20.6 |
| *Mitra idae* | −70.6 | −35.0 | 1.55 (1,12) | .24 | 17.8 | 3.47 (1,12) | .087 | 28.9 |
| *Murexiella santarosana** | −86.3 | −62.8 | 3.42 (1,8) | .10 | 25.7 | 1.00 (1,8) | .35 | 9.1 |
| *Pteropurpura festiva** | −84.2 | −73.6 | 2.87 (1,8) | .13 | 8.7 | 1.11 (1,8) | .32 | 5.2 |
| Echinodermata | | | | | | | | |
| Sea Urchins | | | | | | | | |
| *Lytechinus anamesus*[ar] | −76.6 | −40.4 | 3.14 (1,15) | .08 | 99.8 | 6.29 (1,15) | **.02** | 68.7 |
| *Strongylocentrotus purpuratus* | +0.7 | +47.6 | 0.35 (1,16) | .56 | 23.5 | 4.43 (1,16) | **.05** | 49.7 |
| Sea Stars | | | | | | | | |
| *Asterina* (= *Patiria*) *miniata* | −85.8 | +0.1 | 81.11 (1,16) | **.0001** | 60.9 | 81.1 (1,16) | **.0001** | 82.1 |

* Assumption test not done.

[^] = Deltas (differences between population densities at Impact and Control sites on each survey) are non-additive in the Before period.

[ar] Analysis was done with first-order autoregressive model to correct for serial correlation, but power was calculated from ordinary least-squares model and overestimates true power.

or increased in abundance at the San Mateo kelp forest (Table 3). This resulted in large relative declines at the Impact sites. At the Near Impact site, all 11 species of snails for which an effect size was calculated declined in density relative to the Control. All but one of these relative declines exceeded 50% (Table 4). At the Far Impact site, all snail species for which an effect size could be calculated also showed relative declines in density (Table 5). However, in every case, the relative declines were less than those seen at the Near Impact site.

We performed *t* tests on the data for nine species of snails. Six showed statistically significant declines at the Near Impact site relative to the Control (Table 4). Analysis of variance was appropriate for six of the species. For two of these, the change averaged over the Near and Far Impact sites was statistically significant (Table 5: Period effect). For one, the decline was significantly greater at the Near than at the Far Impact site (Table 5: Period × Site). Below are the results for individual taxa.

*Snails sampled on most pre-operational surveys.*—Four species of snails were counted on most pre-operational surveys (*Conus californicus, Cypraea spadicea, Kelletia kelletii,* and *Mitra idae*). All are benthic predators (Morris et al. 1980) that are ubiquitous in southern California kelp forests (J. D. Dixon, J. Kastendiek, R. O. Smith, and S. C. Schroeter, *personal observations*). The abundances of all four declined at the Near Impact site relative to the Control. The declines were statistically significant for all but *Mitra idae* (Table 4).

These relative declines were brought about by two different patterns of change in abundance. One, illustrated by *Conus californicus,* was a decline in abundance at the Impact sites accompanied by an increase at the Control (Fig. 3). The other, illustrated by *Mitra idae,* was an increase at the Control, accompanied by little or no change at the Impact sites (Fig. 4).

*C. californicus* and *K. kelletii* were both more abundant at the Impact sites than at the Control site during the Before period. Their average abundance declined at both the Near and Far Impact sites during the After period. The decline was greater at the Near Impact site for both species, but there was not a significant Period × Location interaction (Table 5), indicating power plant effects of similar magnitude at both sites.

Although *M. idae* changed in relative abundance similarly to the other three species, neither the effects of Period (Tables 4 and 5) nor the Period × Location interaction were statistically significant (Table 5). However, the power for all tests was very low (Tables 4 and 5).

*Snails sampled on only two pre-operational surveys.*—Five snail taxa were analyzed separately because they were only sampled near the end of the Before period. As a consequence, the assumptions underlying the hypothesis tests could not be adequately tested.

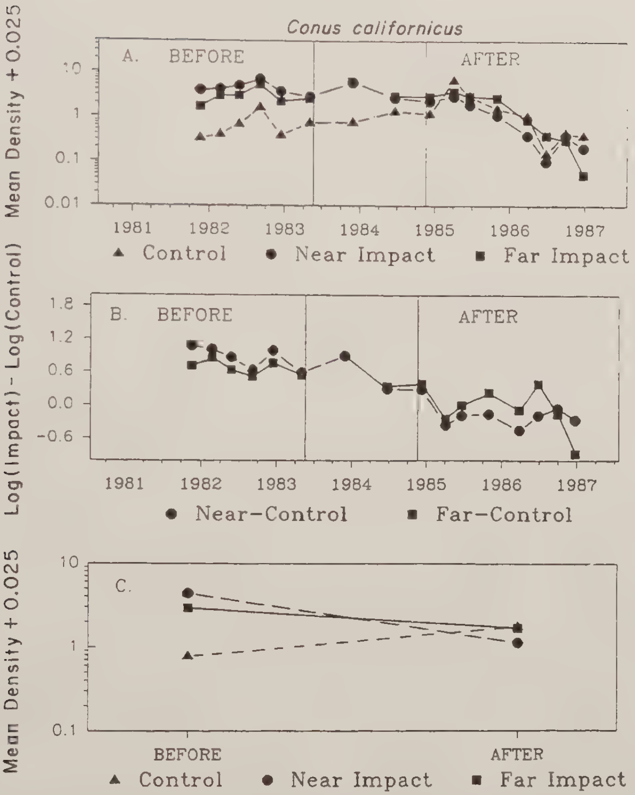

FIG. 3. Changes in the abundance of *Conus californicus* in a kelp forest off the coast of Southern California, in the vicinity of the cooling-water discharge of the San Onofre nuclear power plant. (A) Average density at the Near Impact (SOKU), Far Impact (SOKD), and Control (SMK) sites during the preoperational (Before), interim, and operational (After) periods. Each point is the mean from 40 1-m$^2$ quadrats plus the constant, *C*, specified in the ordinate labels of graphs A and C. (B) Delta plot. Difference in the logs of the average density (mean + *C*) at the Impact and Control sites. These are the data used in the *t* test and the analysis of variance. (C) Interaction plot. Overall average density in the Before and After periods at the Impact and Control sites.

Standing alone, these results are less convincing evidence for an effect of the generating station than the results from species sampled more often and over a longer time period. However, the patterns are similar to those for the species sampled on many pre-operational surveys and thus tend to corroborate the hypothesis of a power plant effect.

*Maxwellia gemma, Murexiella santarosana,* and *Pteropurpura festiva* are benthic predators; *Nassarius* spp. are scavengers; and *Tegula aureotincta* is an herbivore (Morris et al. 1980). The abundance of all five taxa declined at the Impact sites relative to the Control (Tables 4 and 5). Relative declines were brought about by changes in abundance similar to those seen for *C. californicus,* namely a decrease at the Impact site and an increase or no change at the Control during the After period (Table 3). Relative declines exceeded 80% at the Near Impact site for four of the species (*M. gemma, M. santarosana, P. festiva,* and *T. aureotincta*), and were statistically significant for all but *P. festiva* (Table 4). Anovas were performed on data for *M. gemma, M. santarosana,* and *P. festiva.* The declines were larger at the Near Impact site but the Period × Location interaction was only significant for *M. gemma* (Table 5). The power to detect a Period × Location interaction was low for the remaining two species (Table 5).

### *Echinoderms*

Data for the two sea urchins and a sea star passed the assumptions for the *t* test and the analysis of variance. All three are common inhabitants in southern California kelp forests. White sea urchins, *Lytechinus anamesus,* are abundant in the San Onofre region, particularly along the outer edges of the kelp forests (Schroeter et al. 1983). They often move about a great deal and graze on both drifting and attached algae (Leighton 1971, Dean et al. 1984, 1988), and prey on other urchin species (Coyer et al. 1987). White sea urchins were most abundant at the Impact sites in the

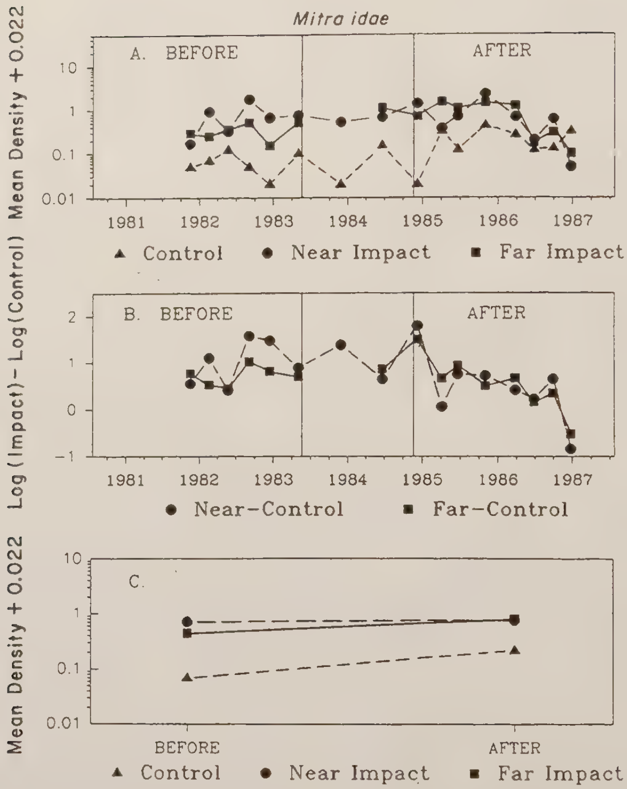

FIG. 4. Changes in the abundance of *Mitra idae* in a kelp forest off the coast of southern California, in the vicinity of the cooling-water discharge of the San Onofre nuclear power plant. See Fig. 3 legend for details.

Before period (Table 3). The patterns of relative change for *L. anamesus* were driven by changes in abundance similar to those seen for *Mitra idae* (Fig. 4). There were substantial increases in density at all the sites during the After period (Table 3). However, the proportional increase was much larger at the Control site, and resulted in relative declines at both of the Impact sites. The relative decline at the Near Impact site was statistically significant and larger than the one at the Far Impact site (Tables 4 and 5). Changes in the abundance of *L. anamesus* were caused by both recruitment and immigration. There was substantial recruitment of recently settled individuals in both the San Onofre and San Mateo kelp forests in the fall and winter of 1981–1982, 1983–1984, and 1984–1985, and immigration of larger animals, especially at the Control site during the last two operational surveys in 1986 (S. C. Schroeter, J. D. Dixon, J. Kastendiek, and R. O. Smith, *unpublished data*). We were concerned that large, site-specific stochastic fluctuations in density due to immigration of adults unrelated to the operation of the power plant might have strongly affected the patterns we observed. To examine this possibility, we excluded data from the last two surveys and re-ran the $t$ test. This resulted in a somewhat lower effect size (−65% vs. −76%) but a much higher significance level ($P$ = .0008 vs. .018).

The purple urchin, *Strongylocentrotus purpuratus*, is another common grazer in southern California kelp forests. Purple urchins were common at the Control site, but uncommon to rare at both Impact sites during both operational periods (Table 3). There were small declines in average density at the Control and Near Impact sites and a small increase at the Far Impact site in the After period. Neither the $t$ test nor the analysis of variance showed statistically significant effects suggestive of an effect of the power plant (Tables 4 and 5). The significant interaction resulted from the greater relative increase at the more distant impact site, which is not consonant with an effect of the discharge.

The bat star, *Asterina* (= *Patiria*) *miniata*, was the only one of the eight species of sea stars sampled during the study (Table 2) that was abundant enough to test for effects of the generating station. As was the case for

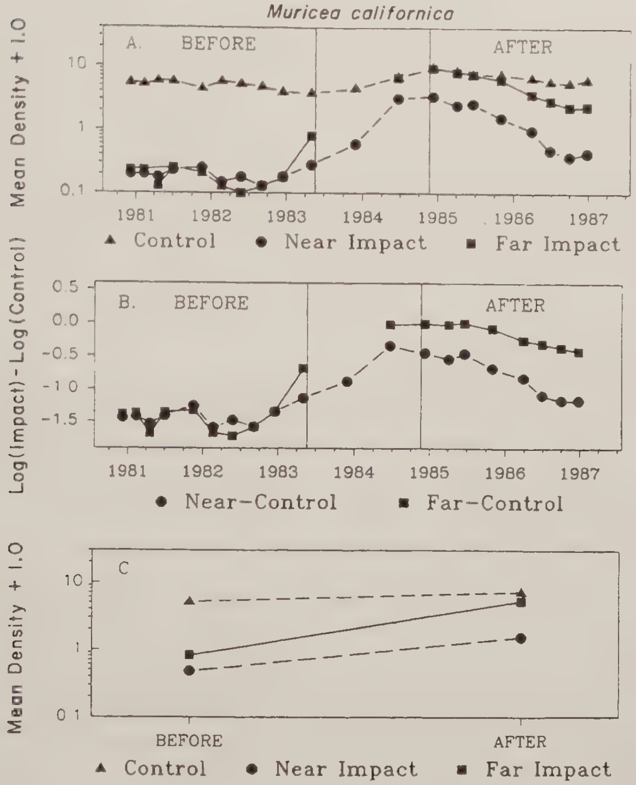

FIG. 5. Changes in the abundance of *Muricea californica* in a kelp forest off the coast of southern California, in the vicinity of the cooling-water discharge of the San Onofre nuclear power plant. See Fig. 3 legend for details.

most of the snails (cf. Fig. 3), patterns of relative change in *A. miniata* were due to declines at the Impact sites (Table 3). In the Before period bat stars were about twice as abundant at the Near Impact site as at the Far Impact site, and densities at the Control site were about 10-fold lower. From 1981 through 1984 subtidal populations of sea stars in southern California were struck with a series of bacterial epizootics that decimated shallow populations (S. C. Schroeter, J. D. Dixon, R. O. Smith and J. E. Hose, *unpublished data*). During the operational period there was some recruitment of small individuals at all sites. The net result was that the average abundance at the Control site did not change from the Before to the After periods, whereas the average abundance was lower at both Impact sites during the After period. The relative decline at the Near Impact site was statistically significant (Table 4) and was greater than at the Far Impact site, where the relative declines were also substantial (Table 5).

### *Large sessile invertebrates*

Data from two species of large sessile invertebrates were suitable for either the *t* test or the analysis of variance. One, the sponge *Tethya aurantia,* was analyzed both with the *t* test and the analysis of variance. Data for the other, the gorgonian coral *Muricea californica,* was analyzed with the *t* test, but failed the assumptions for the analysis of variance (Table 1).

*T. aurantia* occurred in small numbers at all the sites throughout the study. During the Before period, densities were highest at the Near Impact site and lowest at the Far Impact site. From the Before to the After period, there were modest declines in abundance at the Near Impact and Control sites and no change at the Far Impact site (Table 3). This pattern resulted in a small relative increase at the Near Impact site that was not statistically significant (Table 4). Power for this test was very high. There was a larger relative increase at the Far Impact site resulted in significant Period and Period × Location effects (Table 5). This pattern resulted from changes at the Far Impact station that, if caused by the power plant, require more complicated mechanisms than for cases where effects fall off with distance.

The patterns of relative changes for the gorgonian coral, *Muricea californica,* resulted from large increases

TABLE 6. Results of $t$ test on seston flux near the cooling-water outflow from the San Onofre (California) nuclear power generating plant, using a first-order autoregressive model (AR1) to correct for serial correlations.*

| | Seston flux (mm/day) | | | | | | |
|---|---|---|---|---|---|---|---|
| Period | SOKD (Far Impact) | SOKU (Near Impact) | SOKU− SOKD | $N$ | $P$ value | Effect size (%) | Power (%) |
| Before | 7.62 | 7.65 | 0.03 | 31 | .001 | +45.8 | ≈100 |
| After | 7.47 | 11.16 | 3.69 | 21 | | | |

* The Near Impact (SOKU) site is compared to the Far Impact (SOKD) site because no transformations were found that produced additivity for the Control (SMK) vs. Near Impact (SOKU) comparison. Daily seston flux was calculated from biweekly accumulations in sediment traps, and transformed as $\log(x + 0.53)$ to produce additivity. $N$ = number of 2-wk periods. Power to detect a 50% change at SOKU was calculated with uncorrelated errors and is therefore somewhat inflated.

at the Impact sites coupled with more modest increases at the Control (Table 3). *M. californica* was an order of magnitude more abundant at the Control site than at the Impact sites during the Before period. There was substantial recruitment in the San Onofre kelp forest during the Interim period, but only modest recruitment at San Mateo. During the After period there was a general decline in density at San Onofre, but little change at the Control site (Table 3). The relative increase at the Near Impact site, due in large measure to the higher recruitment during the Interim period (Fig. 5), was statistically significant (Table 4). The data were not appropriate for an analysis of variance.

### *Seston flux, irradiance, and substrate changes*

The discharge of Units 2 and 3 of the San Onofre Nuclear Generating Station often creates turbid plumes over the San Onofre kelp forest. These plumes are the likely cause of changes in two of the physical variables, seston flux and underwater irradiance, at the Impact sites relative to the Control. Analysis of the data from the seston traps indicates an increase in the flux of seston near the bottom by 46% at the Near compared to the Far Impact site (Table 6; MRC 1989*b*). The increase in seston flux relative to the Control was probably even higher, since the Far Impact site is also under the plume part of the time. There was, however, no transformation that produced additivity for the Control − Near Impact comparison, so no effect could be estimated. The discharged cooling waters also resulted in a reduction in underwater irradiance (photon flux density) of $\approx 0.65\ \mathrm{mol\cdot m^{-2}\cdot day^{-1}}$ at the Impact sites relative to the Control when currents were running downcoast and bringing the plume over the San Onofre kelp forest (Table 7) (Reitzel et al., *in press*). On average, downcoast current days comprise ≈60% of the total.

In contrast to seston flux and irradiance, the operation of the power plant had no effect on water temperature (MRC 1989*a*). The data are of further interest because they allow us to look for any differential effects of a major oceanographic event, the strong El Niño of 1982–1984, on the Impact and Control sites. This is important since the El Niño occurred just before and during the startup of the power plant. The analysis indicates that temperatures were elevated by an average of ≈2°C during the El Niño, after which they returned to the pre-El Niño values. The changes at the Control and Impact sites were virtually identical (Table 8).

From the Before to the After period at both the Control and Far Impact sites there was a decline in the proportion of the exposed sea floor composed of unconsolidated substrates. In contrast, there was a substantial increase in sediment cover at the Near Impact site (Fig. 6). Sometime between July and October 1985 several of the sampling quadrats were covered with mud. The mud compacted and became armored with coarser materials. This deposit of muddy sand accreted with time (Table 9), resulting in an increase in the

TABLE 7. Comparison of average underwater quantum irradiance (photon flux density levels, using $t$ tests*). Irradiance at SOK is the average of values from three stations spread throughout the San Onofre kelp forest, those at SMK are from one San Mateo station. The $P$ value is for the $t$ test of a difference in the average deltas (SOK − SMK) between the Before and After periods.

| | Average daily irradiance ($\mathrm{mol\cdot m^{-2}\cdot d^{-1}}$) | | | |
|---|---|---|---|---|
| Period | SOK | SMK | Reduction due to impact ($\mathrm{mol\cdot m^{-2}\cdot d^{-1}}$) | $P$ value |
| Before | 1.25 | 1.34 | −0.65 | <.003 |
| After | 1.34 | 2.08 | | |

* The $t$ tests were done using a first-order autoregressive model (AR1). Results are based on analyses by Reitzel et al., *in press*.

TABLE 8. Average daily bottom temperature at the Control and the Near and Far Impact sites before, during, and after the 1982–1984 El Niño. The period before El Niño is from October 1981 through September 1982; during El Niño is from October 1982 through September 1984; after El Niño is from October 1984 through September 1986. The table is reproduced from MRC 1989*a*.

| | Average daily temperature (°C) | |
|---|---|---|
| Period | SMK (Control) | SOK* (Impact) |
| Before El Niño | 14.6 | 14.8 |
| During El Niño | 16.3 | 16.6 |
| After El Niño | 14.6 | 14.7 |

* SOK = The average of values from three stations spread throughout the San Onofre kelp forest, off southern California.

TABLE 9. Average percentage of sea floor covered by muddy sediments at the Control (SMK), Near Impact (SOKU), and Far Impact (SOKD) sites from June 1985 to the end of the study.

| | % cover of muddy sediments | | |
|---|---|---|---|
| Date | SMK (Control) | SOKU (Near Impact) | SOKD (Far Impact) |
| June 1985 | 0.0 | 0.0 | 0.0 |
| October 1985 | 0.0 | 14.7 | 0.0 |
| March 1986 | 0.0 | 29.5 | 6.8 |
| June 1986 | 0.0 | 30.6 | 6.8 |
| September 1986 | 0.0 | 35.0 | 3.9 |
| December 1986 | 0.0 | 44.2 | 0.2 |

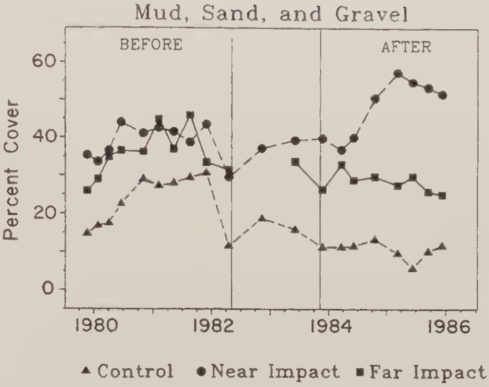

FIG. 6. Average percentage of cover of unconsolidated substrates (mud, sand, and gravel) at the Near Impact (SOKU), Far Impact (SOKD), and Control (SMK) sites in the vicinity of the cooling-water discharge of the San Onofre (California) nuclear power plant, during the preoperational (Before), interim, and operational (After) periods.

percentage of cover of unconsolidated materials at the Near Impact site from ≈40% to between 50 and 60% toward the end of the study (Fig. 6). During the After period mud was frequently observed elsewhere in the San Onofre kelp forest, including the Far Impact site (Table 9), but these deposits were ephemeral.

The results of the $t$ tests using only mud-free quadrats at the Near Impact site were essentially the same as the analysis using all the data (Table 10). There were significant relative declines of snails (*Conus californicus, Cypraea spadicea, Kelletia kelletii, Maxwellia gemma, Murexiella santarosana,* and *Tegula aureotincta*), white sea urchins, *Lytechinus anamesus,* and bat stars, *Asterina miniata.* The gorgonian *Muricea californica* again showed a significant relative increase.

TABLE 10. Results of $t$ tests on abundances of large kelp forest invertebrates comparing the Near Impact (SOKU) to the Control (SMK) sites. Only quadrats that were free of mud were used in the analysis.

| | Number of surveys | | | | |
|---|---|---|---|---|---|
| Species† | Before | After | $P$‡ | Effect size (%) | Power (%) |
| Porifera | | | | | |
| *Tethya aurantia* | 10 | 6 | **.034** | +80.6 | 51.8 |
| Cnidaria | | | | | |
| *Muricea californica* | 10 | 6 | **<.001** | +393.4 | 85.7 |
| *Muricea fruticosa* | 10 | 6 | .090 | +174.6 | 2.9 |
| Mollusca | | | | | |
| *Astraea undosa* (T,$^{ar}$) | ... | ... | ... | −85.5 | ... |
| *Conus californicus* | 6 | 6 | **<.001** | −90.5 | 62.0 |
| *Crassispira semiinflata* (T) | 5 | 5 | ... | −82.0 | ... |
| *Cypraea spadicea* | 9 | 6 | **.039** | −59.5 | 18.2 |
| *Kelletia kelletii* | 10 | 6 | **.013** | −51.3 | 69.1 |
| *Maxwellia gemma** | 2 | 6 | **.006** | −91.7 | 15.5 |
| *Mitra idae* | 6 | 6 | .280 | −58.0 | 11.8 |
| *Murexiella santarosana** | 2 | 6 | **.002** | −87.9 | 23.8 |
| *Nassarius* spp.* | 2 | 6 | .332 | −54.0 | 8.5 |
| *Pteropurpura festiva** | 2 | 6 | .093 | −86.1 | 8.6 |
| *Tegula aureotincta** | 2 | 4 | **.027** | −91.1 | 19.0 |
| Echinodermata | | | | | |
| Sea Urchins | | | | | |
| *Lytechinus anamesus*$^{ar}$ | 10 | 6 | **.001** | **−60.6** | **80.2** |
| *Strongylocentrotus purpuratus* | 10 | 6 | **.406** | **−35.3** | **24.2** |
| Sea Stars | | | | | |
| *Asterina* (= *Patiria*) *miniata* | 10 | 6 | **<.001** | −86.3 | 62.7 |
| Urochordata | | | | | |
| *Styela montereyensis* (T) | 10 | 8 | ... | −42.9 | ... |

† T = linear trend in the deltas in the Before period; $^{ar}$ = analysis done with a first-order autoregressive model to correct for serial correlation, but power calculated from ordinary least-squares model and overestimates the true power; * = species for which no assumption tests were done.

‡ $P$ values in bold are <.05.

In addition, the sponge *Tethya aurantia* showed a significant relative increase.

## Discussion and Conclusions

The results of this monitoring study demonstrate two patterns of change in the assemblage of invertebrates in the San Onofre kelp forest that occurred after Units 2 and 3 of the San Onofre Nuclear Generating Station (SONGS) began normal operation. The first was a decline in density, relative to populations at a control site, of a taxonomically diverse group of species. There were statistically significant relative declines in the density of snails (*Conus californicus, Cypraea spadicea, Kelletia kelletii, Maxwellia gemma, Murexiella santarosana,* and *Tegula aureotincta*), a sea urchin, *Lytechinus anamesus,* and a sea star, *Asterina miniata.* The second pattern was an increase in abundance of two species in the San Onofre kelp forest relative to the control populations. These were the gorgonian *Muricea californica* and the sponge *Tethya aurantia.*

How does one judge whether the observed changes in relative density were caused by a human-made perturbation, in this case the cooling-water discharge of a nuclear power plant? The answer depends on confidence in the analyses, consistency of the results, and the weight of the evidence regarding reasonable mechanisms.

Although the BACI design and associated analyses are important tools for assessing environmental impacts, we believe that the case for biological effects of anthropogenic perturbations should not rest solely on the statistical significance of formal hypothesis tests, nor should the results for individual species be evaluated alone. In the absence of a demonstrated causal chain, a convincing case requires that the results for a number of different species tie together and be consistent, that plausible mechanisms for an ecological impact be identified, and that reasonable alternative mechanisms be explored and ruled out.

We believe that the results presented here make such a case. Most species (11 of 14) showed relative declines in density during the After period (i.e., after full-scale operation of the nuclear plant). The average effect size was about −75% at the Near Impact site. Data were appropriate for an analyses of variance for 7 of the 14 species to determine the relative magnitude of the decline at the Near and Far Impact sites. In each case the effect was less at the Far Impact site (average effect size: −52%). This pattern is most convincing for *Conus californicus, Cypraea spadicea, Kelletia kelletii,* and *Mitra idae,* all fairly abundant snails that were sampled 6–10 times in the Before period. However, the pattern of relative decline was very similar for snail species that were only sampled twice in the Before period. Confidence in the pattern was further strengthened by the results for white sea urchins and bat stars, which also showed larger relative declines at the site near the diffusers than at the Far Impact site.

There are plausible mechanisms for the declines. The operation of Units 2 and 3 caused an increase in the flux of fine particles in the water column over the San Onofre kelp forest, especially near the diffusers. There was a 46% increase in seston flux at the Near Impact site relative to the Far Impact site. This undoubtedly resulted in increased flux of fine particles on rocky substrates. The frequent dusting of rocky surfaces with fine inorganic particles and the occasional coating of hard substrates with mud might reduce larval settlement, interfere with egg laying (significant to local populations if larvae are short-lived), induce adult emigration, and cause mortality of encrusting sessile prey. The generating station may also have had other, indirect effects on invertebrates. Generating Units 2 and 3 caused a significant reduction in the size and density of the San Onofre kelp forest relative to the San Mateo kelp forest by reducing recruitment of giant kelp, *Macrocystis pyrifera,* probably by reducing irradiance at the sea floor (MRC 1989*b*). The local reduction in the standing stock of giant kelp and the consequent reduction in drift kelp could adversely affect species that utilize it for food, such as white sea urchins (Leighton 1971) and bat stars (Gerard 1976).

Concluding that the power plant has caused the two observed relative increases in density is not as straightforward as for the cases of relative decline. On the one hand, there is a plausible mechanism for the increases. In addition to increasing the local flux of fine inorganic particles, the cooling system takes in, kills, and discharges on the order of thousands of tons of plankton per year (MRC 1988*b*). The resultant organic particles might increase the food available to filter feeders, such as *Muricea californica* and *Tethya aurantia.* On the other hand, the relative increases for both species were greater at the Far than the Near Impact site. Mechanisms involving operation of the power plant could be invoked to account for these patterns, but they are more complicated than mechanisms that account for an effect which falls off with distance. For example, the fine organics may tend to be more concentrated on the bottom at the Far than the Near Impact site because of delays in settlement through the water column. Alternatively, the increased supply of organic particles could have positive effects at both the Near and Far Impact sites, but the increased flux of inorganic particles could have more severe adverse effects (e.g., burial or abrasion) at the Near Impact site.

We have considered three alternative hypotheses unrelated to the operation of the power plant that could potentially explain our results. The first applies to the gorgonian *Muricea californica.* In the case of this species, the differences between the Control and Impact sites in the After period resulted primarily from differences in rates of recruitment from the plankton. Although we did not measure the amount of open space available for settlement, our impression was that there was less substrate available for settlement at the Control than at either Impact site. This raises the reasonable possibility that the results we observed were a function of space-limited recruitment at the Control site rather than an effect of the power plant.

We considered two other hypotheses that apply to all of the species: (1) the Control and Impact sites were affected differently by oceanographic events, particularly the 1982–1984 El Niño, and (2) a natural increase in sediment cover at the Near Impact site produced the observed declines in relative density.

The oceanographic manifestations of the El Niño occurred just before and shortly after SONGS Units 2 and 3 began operation, and resulted in elevated temperatures, depressed nutrient concentrations, and unusually severe storms in the early spring of 1983 (Simpson 1983, Tegner and Dayton 1987, MRC 1989*a*). However, the evidence does not suggest that El Niño contributed significantly to the observed relative changes in population density. For example, in each of the El Niño years the correlation coefficient of bottom temperature between the Control and Impact sites was between 0.91 and 0.96 (MRC 1989*a*). There were no measurable, site-specific changes in physical parameters that parallel and might explain the changes in the invertebrates. Another possibility is that the severe storms in the spring of 1983 interacted with topographical differences between the Impact and Control sites to produce more severe declines at the Impact sites. However, there was more obvious disturbance of the bottom in the San Mateo than in the San Onofre kelp forest during stormy periods (R. O. Smith, S. C. Schroeter, and J. D. Dixon, *personal observations*), and giant kelp mortality was about the same at the two sites during that period (Zabloudil et al. 1989). Therefore it appears that waves associated with the 1983 storms had similar or less destructive effects at San Onofre than at the Control site.

The third alternative hypothesis is that the observed relative changes in population densities resulted from the deposition of mud at the Near Impact site that began in summer 1985. We treat this as an alternative hypothesis because there remains a question as to whether that mud deposition was natural or an effect of the generating station. The deposit of sandy mud that first appeared in October 1985 and that persisted and accreted for the remainder of the study reduced the density of invertebrates in those quadrats that were partially or completely buried. Although this undoubtedly contributed to the decreases in relative density that we observed, it is not a sufficient explanation. This assertion is based on the facts that most species were declining in density at the Impact sites before the mud was deposited, that there were significant, although smaller, relative declines at the Far Impact site in the absence of persistent mud deposits, and that there were relative declines at the Near Impact site in quadrats where there was no mud. Therefore something in addition to a persistent change in substrate composition was responsible for the biological results. We believe that it was the ephemeral deposition of fine particles discussed above. Although not conclusive, there is also considerable circumstantial evidence that the frequent appearance of mud deposits in the San Onofre kelp forest during the After period was itself an effect of the generating station (MRC 1991). That judgment was based on the following observations: (1) the diffusers created a turbid plume over much of the kelp forest, significantly increasing particle flux; (2) the interactions of the discharge and make-up flow and the discharge and stands of giant kelp created stagnation points where there was little water movement, a condition favorable to particle deposition; (3) there were no observations of mud at kelp forests depths during the Before period, except immediately following those large storms that produced heavy fresh water run off; (4) although the After period coincided with a major drought, mud was frequently observed in the San Onofre kelp forest, especially in the upcoast portion near the diffusers, but was rarely encountered elsewhere at similar depths; (5) mud collected from the San Onofre kelp forest had a higher organic content, corrected for particle size distribution, than mud collected in deeper water where it is the characteristic substrate.

In summary, the results of statistical analyses, coupled with studies of oceanographic parameters, provide strong evidence that the operation of the power plant has affected the densities of many invertebrate species in the San Onofre kelp forest. The analyses also indicate that although the effects of the generating units are detectable throughout the San Onofre kelp bed, they are significantly smaller at a distance of ≈1.5 km from the discharges. The evidence for a power plant effect is more convincing for the species that showed relative declines than for the two that showed relative increases. Finally, it is worth noting that only about one third of the species that originally seemed appropriate provided data that were statistically tractable. For most of these, the power to detect a halving or doubling was generally very low. As a result, the only effects that were statistically significant were large (60–90% declines). Therefore, relying only on the statistical analyses would underestimate the number of ecologically significant changes.

As a coda, we would like to summarize the lessons we have learned regarding strategies of environmental impact assessment. The BACI design is a powerful tool to assess whether abundances or other variates of interest have been affected by human perturbations. However, there are limitations to this approach when one is dealing with organisms that live long and recruit infrequently, such as the marine benthic invertebrates in our study. Such characteristics can produce two generic and related problems: serial correlation and low power.

The rates of change of organisms that live many years and recruit sporadically are often so low that sampling frequencies greater than once, or at most, a few times per year, are likely to introduce serial correlations. In most cases, these serial correlations will be positive because observations close in time are likely to be similar. If we falsely assume independence, we will underestimate the error terms in the analysis and inflate the true Type I error rate ($\alpha$) relative to the nominal one. It is possible, in theory, to estimate and correct for such serial correlations (e.g., Durbin–Watson test or time-series analyses). However, for long-lived animals of the type considered in our study, the sample sizes for studies shorter than about 10 yr (5 yr of quarterly surveys each for the Before and After periods) are likely to result in low power to detect serial correlation. Even if we decided to correct for serial correlation with no pre-testing, our supposedly "corrected" analyses would still be biased (Park and Mitchell 1980). Thus, serial correlations and their effects on the Type I error of statistical tests will go undetected or under-corrected. This problem (which afflicts most studies, regardless of statistical model) can be cured by increasing the length of the monitoring period—but we suspect that this will be an infrequently applied remedy because of costs and various other practical constraints. We suggest two possible solutions to the problem. First, there are other population attributes, such as settlement, and size-specific individual growth, fecundity, and survivorship, that often can reasonably be estimated frequently and are less likely to be serially correlated (cf. Osenberg et al., *in press*). Second, field experiments could be conducted with those species that are considered particularly important or that appear to be suffering impacts. The results of such experiments would help identify the mechanisms underlying the density changes, and increase the confidence in the monitoring results. The strongest studies of environmental impacts are those that demonstrate the linkage between physical and chemical perturbations and biological changes. Besides increasing the credibility of the monitoring results, this information could be used by dischargers and regulators to institute physical or operational changes in order to reduce deleterious environmental effects.

The second generic problem is low power of significance tests of impact. Because of the potential problems of serial correlation, increasing sample size usually means increasing the length of the study. This frequently is not an option, both because of increased costs and because the study times required (on the order of 10 or more years) are long relative to regulatory time scales. Two of the possible remedies for serial correlation (use of variates other than abundance, and manipulative experiments) also apply to the problem of low power. At the very least, the magnitude of the problem of low power can be assessed by calculating power and the effect sizes in addition to $P$ values. If one knows both the power of the test and the effect size, one can make informed judgments as to whether the analyses have underestimated the degree of ecologically significant impacts.

The BACI design allows one to test whether there has been a statistically significant change in abundance (or some other variable) at an Impact site relative to one or more Control sites. Most studies of environmental impacts have a single impact site. It has been argued that such a design runs the risk of confusing natural Period × Location interactions with an impact (Hurlbert 1984). Stewart-Oaten et al. (1986) point out that the chances of such misinterpretation are reduced by sampling the paired differences between Control and Impact sites repeatedly in the Before and After periods. Nevertheless, the possibility that natural Period × Location interactions may mimic an environmental impact should be considered. We attempted to address the problem in three ways: by the use of more than one Impact site, by examining a number of potential target species, and by seriously evaluating plausible alternative hypotheses.

Use of either multiple Control (e.g., Carpenter 1989) or multiple Impact sites increases the chances of distinguishing between natural Period × Location interactions and an environmental impact. However, in the present study, the primary value of multiple Impact sites was not to provide replication in a statistical sense, but rather to provide spatial information that was useful in determining the pattern and extent of the impact. Similar patterns of relative change for a number of species clearly strengthen the evidence for an ecological effect of the impact. It seems to us that analyses that deal with individual species lead to stronger inferences than those that use summary statistics that combine data from the different species. There are two reasons for this. First, similar patterns for a number of species tend to corroborate the conclusion of either the presence or absence of an effect. Second, statistics or indices that do not distinguish among species can't adequately describe the diversity of response.

We think it is clear that determining the "significance" of an effect is not something that should be done by rote (cf. Yoccoz 1991). When considering issues of pollution or human health, sole reliance on a statistical significance level of .05 in a hypothesis test to identify impacts is inadequate. The size of the effects, the weight of all of the evidence, and the costs of falsely implicating (Type I error) or falsely exonerating (Type II error) the presumed polluter must be considered.

In conclusion, we think that our study provides some larger lessons about the general process of impact assessments. Although we were able to detect a number of significant effects, this was primarily because many of the effect sizes were substantially larger than 50% changes. The present study extended over nearly 6 yr, yet the resulting statistical tests generally had low power (<30%) to detect 50% reductions (or doublings) in abundance at the conventional test level of .05. We believe that this will often be the case when sampling populations of relatively long-lived organisms in dynamic natural systems. Many assessment studies are substantially shorter than ours, and we suspect that the design of many impact studies is such that only the grossest effects could be detected. Obviously, it would be a mistake to conclude that there were no, or insignificant, effects based simply on a conventional significance test applied to the results of such a study. Because an increase in effective sample size implies an increased study duration, we cannot generally increase power simply by increasing the resources available for each individual study. The above discussion leads us to conclude that we need to change the standards and types of evidence used to demonstrate an impact, or to accept the fact that effects on the order of 50% changes will often be missed. One solution would be to increase the Type I error rate and thus reduce the Type II error rate; ideally this would be done by balancing the costs of different types of errors. This approach would require some prior idea about the likely size of effects. We believe that intensive studies like ours are generally useful in part because, combined with other relevant information (such as studies of mechanisms), they can provide this type of prior information.

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# CAPACITY UTILIZATION UNDER REGULATORY CONSTRAINTS

Kathleen Segerson and Dale Squires*

*Abstract*—This paper presents a methodology for predicting the effect of quota-type regulatory constraints on capacity utilization for a multiproduct profit-maximizing firm. The approach builds on recent advances in the use of virtual prices to model the effects of rationing. This allows the effects of regulatory constraints to be examined ex ante. The methodology is illustrated through a case study of the imposition of output quotas in an open-access marine fishing industry on the Pacific Coast of the United States. The results suggest that, for certain species, output quotas can cause strong disinvestment incentives.

## I. Introduction

MEASURES of capacity utilization (*CU*) have been used for many years to analyze the current status of the economy, the expansionary or contractionary forces on investment and inflation, and productivity movements. Traditional *CU* measures were based on the notion of maximum possible output. Recently, economists have developed measures derived from the economic theory of the firm and based instead on a notion of optimal output (Berndt and Fuss, 1986; Hickman, 1964; Klein, 1960; Morrison, 1985, 1988; Segerson and Squires, 1990a). These measures assume that some inputs are quasi-fixed and that capacity utilization is determined by the level of the quasi-fixed input(s) relative to the level of output.

Previous studies of theory-based *CU* measures have generally assumed that the industry under study was free from regulatory constraints. An exception is Morrison's (1988) study, which analyzed (among other things) the effect of pollution-control regulations on capacity utilization in the U.S. and Canadian steel industries. The analysis is retrospective, however, since it studied the impacts of regulations that were already in effect.

In many cases, it would be useful to be able to predict the effect of proposed regulations on capacity utilization. Such prospective or ex ante analysis would provide regulators with useful information regarding the likely effect of alternative policies on investment incentives. For example, regulatory production limits on a single product (such as quotas) may cause multiproduct firms to change the volume and mix of their production, which could in turn change investment incentives.[1] Likewise, input use restrictions could affect both output supplies and the demands for unregulated inputs, thereby altering investment incentives. Predictions of these changes would contribute to designing more effective public policies regulating capacity and investment.

If the impacts of regulations on supply are important, output choices must be endogenous in the models that predict those impacts. Previous studies of *CU* have treated output as exogenous, however, focusing on cost-minimization as the behavioral objective of the firm.[2] Thus, to be of use in predicting the effects of regulatory constraints on investment incentives, the standard *CU* measures must be modified to reflect an alternative behavioral assumption, such as profit maximization.

The purpose of this paper is to present a methodology for predicting the effect of quota-type regulatory constraints on capacity utilization for a multiproduct profit-maximizing firm. We develop the methodology in the context of a firm

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[1] In addition to a change in the mix of regulated and unregulated products, if the production limit is applied to a product class, which actually entails several variants of a product, quality upgrading could result, i.e., firms could also adjust their product mix within the category of regulated outputs. We are grateful to an anonymous referee for noting this possibility.

[2] An exception is Squires (1987). See further discussion below.

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that faces possible input or output quotas. Our approach builds on recent advances in the use of virtual prices to model the effects of rationing (e.g., Neary and Roberts, 1980). We then illustrate the methodology by predicting the effect of output quotas in a multiproduct fishing industry on the Pacific Coast of the United States. In the context of our example, a special case of profit maximization, namely, revenue maximization, is assumed, since for many fisheries all inputs are effectively fixed in the short run.

Although implementation of the methodology is developed through a case study of a marine fishing industry, the approach should be widely applicable to analyses of *CU* for any industry with profit-maximizing multiproduct firms facing input or output constraints. For example, it could be applied in the context of agriculture where farms face potential water rationing or restrictions on the use of chemical fertilizers or pesticides or potential output quotas to regulate production.[3] Alternatively, in the context of international trade, it could be used to analyze the effects of export quotas or voluntary export restrictions. Other possible applications include the impacts of policies that would ban the production of a particular output or use of a particular input (for health or environmental reasons) and fiscal policies that might result in credit rationing.

## II. Measures of Capacity Utilization

Capacity utilization measures have only recently been developed from the theory of firm behavior (Klein, 1960; Hickman, 1964; Morrison, 1985, 1986; Berndt and Fuss, 1986).[4] For single product firms, the primal measure of *CU* is defined as $CU^Y = Y'/Y^*$, where $Y'$ is actual output and $Y^*$ is the long-run equilibrium output level under cost minimization, i.e., the output level at which the short-run and long-run average cost curves are tangent. *CU* can be equivalently measured in terms of the cost gap that exists when $Y'$ is not equal to $Y^*$ (Morrison, 1985). This dual *CU* measure contains information on the difference between the current temporary equilibrium and the long-run equilibrium in terms of the implicit costs of divergence from long-run equilibrium. It is defined as $CU^C = C^*/C$, where $C$ is the firm's actual cost and $C^*$ is its shadow cost.

*CU* has traditionally been measured for single-product firms. Segerson and Squires (1990a) considered *CU* measurement for multiproduct firms and found that the extension of the single-product primal measure to the multiproduct case can be problematic because a scalar measure of output does not generally exist.[5] However, a dual measure of *CU* for the multiproduct firm that is directly analogous to the single-product measure can be easily defined.

Measures based on the assumption that the firm's objective is cost minimization are particularly well-suited when production strategies strive for economies of scale arising from high-volume focused production of standardized goods in anticipation of a stable market demand. These mass production firms may be concerned primarily with costs in order to meet competition from low-cost producers (Abegglen and Stalk, 1985; Dosi, 1988; Skinner, 1985). If production is not fixed, however, choice of output levels must be considered. This consideration seems particularly important for multiproduct firms, which often seek to adjust their product line in response to a shifting, more disaggregated market (Abegglen and Stalk; Dosi; Stalk, 1988).[6] In addition, it is a potentially important component of a firm's regulatory response.

If multiproduct firms choose output levels to maximize profit, then the shadow value of the quasi-fixed input[7] ($Z$) will be the change in restricted profit resulting from a marginal change in $Z$, i.e., the derivative of the restricted profit function ($H$) with respect to $Z$ (Lau, 1976). A dual $CU$ measure can then be defined in terms of the profit gap (rather than the cost gap) that results from being out of long-run equilibrium (Squires, 1987).[8] In particular, we can define $CU^S = S/S^*$, where $S$ is the actual profit and $S^*$ is the shadow value of profit. Thus,

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[3] Constraints have been used in many other industries as well, including trucking, railroads, airlines, and banking.

[4] An alternative approach, based on the concept of maximum output, has been used for many years. For a discussion, see Morrison (1985).

[5] A consistent scalar measure of output in multiproduct firms exists if all outputs are homothetically separable from inputs. In this case, a direct analogue of the single-product primal measure of *CU* can be developed for the multiproduct firm. When the technology is not homothetically separable, Segerson and Squires (1990a) suggest two alternative ways of defining a primal *CU* measure. However, since both make restrictive assumptions, namely, that outputs move along a ray (giving a ray measure of *CU*) or that only one output adjusts (giving a partial measure of *CU*), we have chosen to focus here on dual measures, which do not require these assumptions.

[6] Industries where such firms are likely to be important include mini-mill steel, machine tools, metal working, medical equipment, high-end apparel, and increasingly, automotive production.

$$CU^S = \frac{H(P,W;Z) - W_Z Z}{H(P,W;Z) - W_Z^* Z} = 1 + \frac{(W_Z^* - W_Z)Z}{H(P,W;Z) - W_Z^* Z} \quad (1)$$

where $H(P,W;Z)$ is the restricted profit function, $S^* = H(P,W;Z) - W_Z^* Z$, $P$ is a vector of competitive prices for $M$ outputs, $W$ is a vector of competitive prices for $N$ variable inputs, $W_Z$ is the market or rental price for $Z$, and $W_Z^* = H_Z$.

## III. The Effects of Regulatory Constraints

Given data on variable input and output prices and the level of the quasi-fixed factor, the restricted profit function can be estimated and used to calculate either of the two alternative dual measures of $CU$ discussed above. If the firm was not subject to any regulatory constraints during the sample period, these measures provide information on investment incentives in the absence of regulation.[9] In this section, we suggest a methodology for predicting how a regulatory constraint subsequently imposed would affect those investment incentives through changes in $CU$.

We consider first the case of an output quota, where the output of some product, say $Y_1$, is restricted to be less than or equal to some exogenous level, $y_1$.[10] Because the estimated restricted profit function is dependent on prices rather than output levels, it is not possible to incorporate the output constraint directly into the $CU$ measure. However, as noted by Weitzman (1974), primal and dual production constraints are theoretically equivalent in a static, full-information, deterministic setting. Thus, through the use of "virtual prices" (Neary and Roberts, 1980), the quantity constraint can be transformed into a price constraint, which in turn can be directly incorporated into the $CU$ measures.

More specifically, the effect of the quantity constraint on $CU$ can be determined by calculating the new shadow price of the quasi-fixed input, i.e., the shadow price with the regulation, and using this new price to calculate a post-regulation $CU$ measure. If the production constraint is binding and the demands for all other products are perfectly elastic,[11] then the shadow price under regulation can be calculated as follows:

(a) derive the supply function for the regulated output from the restricted profit function $H(P, W; Z)$ using Hotelling's Lemma, i.e., $Y_1^* = H_1$, where $Y_1^*(P, W; Z)$ is the profit-maximizing level of output 1;
(b) given the prices of all other outputs and the variable inputs and the level of $Z$, find the level of $P_1$ for which $Y_1^* = y_1$, which gives the virtual price $p_1$ corresponding to the quantity constraint; and
(c) calculate the post-regulation shadow price of $Z$ as $H_Z$ evaluated at the price vector $(p_1, P_2, \ldots, P_M, W, Z)$.

This new shadow price for $Z$ can then be used to calculate the level of $CU$ that would exist under the regulation.[12]

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[7] We assume throughout that there is a single quasi-fixed factor. Although the definition of $CU$ can be easily extended to include multiple quasi-fixed factors, its interpretation becomes unclear in this context since it is possible to have $CU = 1$ even if the actual prices of the quasi-fixed factors do not equal their shadow values (e.g., if there are offsetting effects). The implications of this for investment incentives are unclear. Finally, the model of a single, aggregate quasi-fixed input has been used elsewhere (Diewert, 1974; Kirkley and Strand, 1988) and is appropriate for our case study. For these reasons, we consider only this case in our conceptual model.

[8] This suggests that theory-based measures of $CU$ are not unique, but instead depend on the underlying behavioral assumption.

[9] In general, when capacity utilization exceeds one, there is an incentive for the firm to invest, i.e., increase the level of its quasi-fixed factor. Likewise, capacity utilization less than one implies disinvestment incentives. This interpretation assumes, however, that output is expected to remain at its current level, i.e., that the current output level is not the result of a temporary variation.

[10] We assume that this quota is strictly binding, i.e., that in the absence of the quota the chosen level of $Y_1$ exceeds $y_1$.

[11] This assumption is appropriate in many applications, including our empirical example. If demand were not perfectly elastic, imposition of the quota on one product could change other product prices through shifts in their supply curves. Predicting these other price changes would require information about the demands for these products.

It should be clear that the effect of an input restriction could be found in an analogous way, i.e., by deriving the corresponding virtual price for the input constraint (the price at which the unconstrained demand for the input equals the restricted level) and evaluating $H_Z$ at that virtual price and all other actual prices.

Note that, in calculating the effect of input or output constraints on $CU$, we hold the quasi-fixed factor at its actual (i.e., pre-regulation) level. This should not, however, be interpreted as suggesting that the firm could not or would not change the level of its quasi-fixed factor in response to the regulation. On the contrary, given regulatory lags, it is likely that the firm would be able to adjust its level of $Z$ in response to the regulation, prior to deciding on the levels of its outputs and variable inputs. Nonetheless, it is appropriate to hold $Z$ constant in the above calculations, since it is only by assessing how actual costs (or profits) compare to their shadow values at the *current* level of $Z$ that we can determine the impact of the regulation on the firm's incentives to change that level.[13]

Finally, the above methodology allows the long-run equilibrium level of the quasi-fixed input under the regulation to be determined. Since the long-run equilibrium level is the level at which the shadow price of the input equals its actual (market) price, its level under the regulation can be determined by solving

$$H_Z(p_1, P_2, \ldots, P_M, W, Z) = W_Z \quad \text{for } Z.$$

## IV. An Application

One multiproduct industry for which policymakers often consider the imposition of regulatory constraints is the fishing industry. It is well known that the open access nature of the fishing industry can lead to over-exploitation of the resource stock, excess investment and reduced harvests and incomes (Gordon, 1954). Possible policy responses include license limitations, which restrict the number of vessels with access to the resource, and harvest quotas, which limit allowable catches.[14] Since most fisheries are characterized by multiproduct production, regulations keyed to a single species will have spillover effects on other species. Efforts to enhance the stock of one species might lead to pressures on other resource stocks. These combined direct and indirect effects of the regulations could either increase or decrease investment incentives as reflected in $CU$. Information on how $CU$ is affected would help regulators design policies consistent with overall objectives relating to resource use and investment (Young, 1988).

The above methodology was used to study capacity utilization in a trawl fishing industry on the Pacific Coast of the United States. This industry is comprised of many multiproduct firms, i.e., relatively small and unspecialized vessels that are diversified in their product mix. At the beginning of each fishing trip, vessel operators key production directly to the market (without stockpiling products in anticipation of future demand), given vessel and resource abundance constraints and relative prices. In addition, inputs on the vessel are largely fixed because boats are away at sea where input levels cannot be readily altered. Thus, a special case of profit maximization, namely, revenue maximization, is the appropriate behavioral objective for a fishing trip once a resource stock area has been determined (Kirkley and Strand, 1988).[15] Furthermore, since vessel size or capital stock is fixed at the trip level and largely determines the level of other inputs over this short production period of one to four days, the input bundle can be specified as a single, composite input, proxied by vessel size.[16]

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[12] Note that, when the profit-gap measure is used to predict the impact of the regulation on $CU$, the restricted profit function $H(P, W, Z)$ should also be evaluated at the virtual price for the regulated output.

[13] We emphasize this point since one reviewer of an earlier version of this paper seemed to suggest that holding $Z$ constant in the calculation of $CU$ was inappropriate if the firm could adjust $Z$ in response to the regulation, suggesting that our methodology is applicable only to unanticipated regulations imposed immediately, i.e., before any possible adjustment in $Z$. As stated in the text, however, it is not the *actual* adjustment of $Z$ that is of interest, but rather the *incentive* for adjustment. That incentive can be determined from our methodology even if the firm anticipates the regulation and actually responds to it prior to choosing its output and variable input levels.

[14] Other policies, such as individual transferable quotas (ITQs), may be more efficient as means of maximizing social welfare (Waugh, 1984). However, the actual choice of policies is usually dominated by biologists, who may have objectives other than efficiency and tend to prefer quotas or caps on harvest rates. We thus analyze quotas here not because they are necessarily efficient but rather because they are often used in practice.

[15] See also Squires and Kirkley (1991) for a discussion of the use of revenue functions to model fisheries' production technologies.

In the special case where all inputs are quasi-fixed (so that variable costs are zero), the cost-based measure of capacity utilization takes a particularly simple form, namely,

$$CU^C = W_Z^*/W_Z, \tag{2}$$

where $W_Z^*$ and $W_Z$ are the shadow and actual prices of the quasi-fixed input, respectively. In addition, it can be easily shown that the elasticity of $CU$ with respect to $P_i$ depends directly on the product-specific scale elasticity[17] ($e_{iZ} = d\ln(Y_i)/d\ln(Z)$), weighted by the ratio of revenue from output $i$, $P_iY_i$, to the shadow cost of $Z$, $W_Z^*Z$ (see Segerson and Squires, 1990b). Thus, the larger the contribution of $Y_i$ to total revenue and the size of this revenue relative to $W_Z^*Z$, the greater the sensitivity of $CU^C$ to a change in $P_i$. Furthermore, a large scale elasticity implies that $CU^C$ will be sensitive to changes in the price of product $i$. These relationships will be useful below in interpreting the differences in the effects of quotas on different products.

### *A. The Empirical Model*

The revenue-maximizing vessel-level production process for each fishing trip can be modeled by a nonhomothetic generalized Leontief revenue function. With symmetry imposed, so that $a_{ij} = a_{ji}$ for $i$ not equal to $j$, it is written (Kirkley and Strand):[18]

$$\begin{aligned} R(P;Z) = {} & \sum_i \sum_j a_{ij}[P_iP_j]^{1/2}Z + \sum_i a_iP_iZ^2 \\ & + \sum_i \sum_k b_{ik}D_kP_iZ \\ & + \sum_i \sum_l g_{il}E_lP_iZ, \end{aligned} \tag{3}$$

where $D_k$ is the $k^{\text{th}}$ of two home port dummy variables for Brookings and Crescent City and $E_l$ is the $l^{\text{th}}$ of three quarterly dummy variables for winter, spring, and fall. The area dummy variables account for spatial variations in access to resource stocks, species abundance, and port effects on prices. The quarterly dummy variables account for intertemporal variations in the technological constraints of weather and resource abundance. $Z$ represents the capital stock or composite input, measured by a vessel's gross registered tonnage ($GRT$). Note that the presence of output cross-price interaction terms in (3) allows for the possibility of jointness-in-inputs, which gives rise to economies of scope.[19]

Input-compensated, revenue-maximizing product supply equations $Y^*(P;Z)$ are given by Hotelling's Lemma (McFadden):

$$\begin{aligned} \partial R(P;Z)/\partial P_i &= Y_i^*(P;Z) \\ &= \sum_j a_{ij}[P_j/P_i]^{1/2}Z + a_iZ^2 \\ &\quad + \sum_k b_{ik}D_kZ + \sum_l g_{il}E_lZ. \end{aligned} \tag{4}$$

Linear homogeneity in prices is automatically satisfied with this functional form.

The shadow price of the quasi-fixed factor is given by

$$\begin{aligned} \partial R(P;Z)/\partial Z &= W_Z^* \\ &= \sum_i \sum_j a_{ij}[P_iP_j]^{1/2} \\ &\quad + 2\sum_i a_iP_iZ \\ &\quad + \sum_i \sum_k b_{ik}D_kP_i \\ &\quad + \sum_i \sum_l g_{il}E_lP_i. \end{aligned} \tag{5}$$

This shadow value depends upon the product prices $P_i$, and the level of the quasi-fixed input,

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[16] More formally, we assume Leontief separability of all the inputs over the short production period. Any input variation is likely to be unplanned and not systematic. See Kirkley (1986) and Kirkley and Strand (1988) for a discussion of this assumption.

[17] See Kirkley (1986) for a discussion of product-specific scale elasticities.

[18] Diewert (1974) and Laitinen (1980) provide further development of the revenue function. Kirkley and Strand (1988) provide one of the first empirical applications.

[19] In our application of the model, we used a likelihood ratio test to test for nonjointness-in-inputs throughout the product set. The null hypothesis was rejected. For a more detailed discussion of jointness-in-inputs, see Baumol, Panzar and Willig (1982), Squires (1987), and Kirkley and Strand (1988).

$Z$. If the model extended beyond a single year, the impact of exogenous technical change could readily be included.

The impact of changes in product prices upon $W_Z^*$ can be evaluated by the elasticity of $W_Z^*$ with respect to changes in the price of $P_i$, i.e.,

$$\begin{aligned}\frac{d\ln(W_Z^*)}{d\ln P_i} &= R_{Zi}\cdot P_i/R_Z\\ &= \Big[a_{ii}P_i + \sum_j 0.5a_{ij}[P_iP_j]^{1/2}\\ &\quad + 2a_iP_iZ + \sum_k b_{ik}D_kP_i\\ &\quad + \sum_l g_{il}E_lP_i\Big]\Big/W_Z^*. \qquad (6)\end{aligned}$$

The above system of supply equations was estimated for a group of vessels in a deep-water fishery off Northern California and Southern Oregon using data for a year without regulation, 1984.[20] All vessels were at least 75 *GRT*. There were a total of 444 observations or fishing trips on the 14 vessels. Six categories of fish were specified as outputs: Dover sole, thornyheads, sablefish, other flatfish, other rockfish, and a residual category, all others. In the "other" categories, individual species were aggregated using Divisia indices.

The input-compensated product supply functions given in equation (4) were initially estimated by ordinary least squares. Heteroscedasticity was found of the form discussed by Parks (1971), in which the error variance is proportional to the squared input level $Z$. Each equation was subsequently divided by $Z$. The system of supply equations was then estimated by Zellner's seemingly unrelated regression procedure and iterated to convergence, with results equivalent to maximum likelihood.[21]

The estimated parameter values of the input-compensated supply equations are presented in table 1.[22,23] Table 2 reports the corresponding own-price input-compensated supply elasticities evaluated at the observed sample mean. These elasticities are nonnegative for all outputs except sablefish, which is negative but statistically insignificant. In addition, the revenue function is increasing and concave in $Z$ at the sample mean.

The own- and cross-price supply elasticities reported in table 2 are uniformly inelastic. Both substitute and complementary relationships are exhibited, although many cross-price supply elasticities are statistically insignificant. This suggests that these firms have relatively little ability to adjust the mix and volume of production in the short run in response to exogenous changes. Some adjustment is possible through changes in fishing location and speed and depth of net tow, but in general the product mix is determined by resource abundance, and most importantly, difficulties in locating the unseen resource. The product-specific scale elasticities reported in the last row of table 2 are all positive and generally inelastic, and are largest for Dover sole, thornyheads, and other rockfish.

Finally, the effects of product price changes on the shadow price of the quasi-fixed factor are reported in table 3. These shadow price elastici-

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[20] Alternatively, we could have estimated both the revenue function (3) and the supply functions (4) jointly. While this would have increased the amount of information used in the estimation, it would have increased the computational costs. In addition, unlike with the translog and normalized quadratic forms, with the generalized Leontief joint estimation is not necessary to recover all of the parameters of the objective function. Thus, following Kirkley and Strand (1988), we estimated only the supply equations.

[21] The functional form is assumed to be exact rather than an approximation, and the errors are from optimization rather than approximation and apply only to the input-compensated supply functions. The problem of zero outputs also arose in a few instances. This creates a limited-dependent variable problem, which may cause bias and non-normality of the residuals. The procedure of Lee and Pitt (1986) can solve this problem by using virtual prices, but is not computationally feasible with the number of variables in this study. While a Box-Cox transformation could be used, we elected not to use it because it assumes a particular form of non-normal disturbances prior to transformation. All estimates instead substituted the small value of 0.1 in when necessary. Sensitivity analysis suggested that the results were relatively robust to the choice of this value. Further reductions to 0.01 and 0.001 reduced the log likelihood value by 0.0996% and 0.246%, respectively. Changes in parameter values were less than 5%.

[22] The explanatory variables in table 1 correspond to the original (uncorrected) form of the supply functions in (4). Thus, the coefficients on Effort correspond to the price effects for $i$ not equal to $j$.

[23] The generalized $R^2$, which measures goodness of fit for the entire system of equations, was calculated for the system of equations prior to the heteroscedasticity correction. It is computed as $1 - \exp[2(L_0 - L_1)/N]$, where $L_0(L_1)$ is the sample maximum of log-likelihood when all slope coefficients equal zero (unconstrained) and $N$ is the sample size (Baxter and Cragg, 1970). The calculated value of 0.99 indicates a very good fit. However, since this statistic is typically high, it should be interpreted with caution (White et al., 1988).

TABLE 1.—PARAMETER ESTIMATES OF INPUT-COMPENSATED SUPPLY FUNCTIONS

| | Quantity Supplied of: | | | | | |
|---|---|---|---|---|---|---|
| Exogenous Variables | Dover Sole | Thorny-heads | Sable-fish | Other Flatfish | Other Rockfish | All Others |
| Price Ratio * Effort ($a_{ij}$) | | | | | | |
| Dover Sole | 97.27 | 1.88 | −4.55 | −1.59 | −2.03 | 0.65 |
| | (11.78) | (1.98) | (4.82) | (0.87) | (2.69) | (1.18) |
| Thornyheads | | 19.17 | 7.25 | −0.15 | −10.45 | −0.47 |
| | | (4.49) | (2.27) | (0.49) | (1.84) | (0.85) |
| Sablefish | | | 37.43 | 0.97 | −1.80 | −2.07 |
| | | | (7.62) | (0.88) | (1.93) | (1.06) |
| Other Flatfish | | | | 10.15 | 0.03 | 0.14 |
| | | | | (1.13) | (0.35) | (0.23) |
| Other Rockfish | | | | | 74.86 | 0.54 |
| | | | | | (17.21) | (0.34) |
| All others | | | | | | 10.45 |
| | | | | | | (1.55) |
| Other Exogenous Variables | | | | | | |
| Effort Squared | −0.18 | 0.02 | −0.13 | −0.04 | −0.09 | −0.03 |
| ($a_i$) | (0.08) | (0.03) | (0.03) | (0.01) | (0.13) | (0.01) |
| Brookings | −28.98 | 11.53 | 8.10 | 2.43 | 27.17 | −0.04 |
| Dummy ($b_{i1}$) | (7.23) | (3.03) | (3.05) | (0.76) | (11.68) | (1.00) |
| Crescent City | −12.60 | 5.13 | −1.03 | −1.65 | 62.32 | −2.09 |
| Dummy ($b_{i2}$) | (7.26) | (2.97) | (3.02) | (0.76) | (11.60) | (1.08) |
| Winter Dummy | 15.03 | 1.52 | 3.54 | 1.54 | −8.58 | −1.78 |
| ($g_{i1}$) | (8.12) | (3.30) | (3.37) | (0.84) | (12.97) | (1.10) |
| Spring Dummy | 3.63 | −1.93 | −0.99 | 0.31 | 3.90 | −1.51 |
| ($g_{i2}$) | (7.92) | (3.21) | (3.28) | (0.82) | (12.67) | (1.07) |
| Fall Dummy | −17.88 | 1.63 | −2.88 | −1.21 | −10.59 | −0.69 |
| ($g_{i3}$) | (8.71) | (3.54) | (3.62) | (0.91) | (13.93) | (1.19) |

Note: Generalized Leontief functional form. Symmetry in prices has been imposed. Linearized standard errors calculated by the delta method are given in parentheses. Apparent heteroscedasticity required estimation of supply per unit of $Z$, but the above exogenous variables refer to the form in (4).

TABLE 2.—PARTIAL EQUILIBRIUM PRODUCT SUPPLY AND SCALE ELASTICITIES

| | Quantity Supplied | | | | | |
|---|---|---|---|---|---|---|
| Price Change | Dover Sole | Thorny-heads | Sable-fish | Other Flatfish | Other Rockfish | All Others |
| Dover Sole | 0.037 | 0.046 | −0.118 | −0.191 | −0.033 | 0.130 |
| | (0.038) | (0.048) | (0.125) | (0.104) | (0.043) | (0.234) |
| Thornyheads | 0.014[a] | 0.021 | 0.185[a] | −0.018 | −0.165[a] | −0.091 |
| | (0.001) | (0.025) | (0.058) | (0.058) | (0.029) | (0.166) |
| Sablefish | −0.030[a] | 0.149 | −0.018 | 0.099 | −0.024 | −0.364 |
| | (0.001) | (0.047) | (0.132) | (0.089) | (0.026) | (0.177) |
| Other | −0.013 | −0.004 | 0.027 | 0.095 | 0.001 | 0.031 |
| Flatfish | (0.007) | (0.013) | (0.025) | (0.076) | (0.006) | (0.050) |
| Other | −0.014 | −0.204[a] | −0.037 | 0.003 | 0.216[a] | 0.086 |
| Rockfish | (0.017) | (0.036) | (0.040) | (0.033) | (0.035) | (0.054) |
| All Others | 0.004 | −0.008 | −0.039 | 0.013 | 0.006 | 0.190[a] |
| | (0.007) | (0.015) | (0.020) | (0.020) | (0.004) | (0.053) |
| Quasi-Fixed | 0.766[a] | 1.125 | 0.322 | 0.012 | 0.914[a] | 0.563[a] |
| Input | (0.158) | (0.674) | (0.191) | (0.401) | (0.448) | (0.183) |

Note: Calculated at observed sample mean for Eureka in summer. Linearized standard errors calculated by delta method are given in parentheses.

[a] Statistically significant at 1%.

TABLE 3.—SHADOW PRICE ELASTICITIES

| Dover sole | Thorny-heads | Sable-fish | Other Flatfish | Other Rockfish | All Others |
|---|---|---|---|---|---|
| 0.4875 | .2248 | .0517 | .0007 | .2252 | .0103 |

Note: Calculated at observed sample mean for Eureka in the summer following equation (6).

ties, calculated from (6), are all positive, indicating that $CU^C$ will increase with increased product prices. Because the shadow price elasticities are all inelastic, the effect of changes in individual product prices on the firm's implicit marginal valuation of its quasi-fixed factor will be comparatively small. This is consistent with the small own- and cross-price elasticities discussed above. In addition, the small elasticities imply that changes in product prices would be expected to cause relatively small changes in *CU*. The two species with the largest expected changes are Dover sole and thornyheads, since these have the largest shadow price elasticities and two of the largest revenue shares.

### B. *Estimates of Current Capacity Utilization*

The shadow value of the quasi-fixed factor was used to estimate actual capacity utilization for the trawl industry in 1984. Both the cost-gap and the profit-gap measures were calculated. Under 1984 resource conditions and prices, the following estimates were obtained:

$$CU^C = 1.017$$

and

$$CU^S = 1.028.$$

These measures are close to one, indicating that the industry was essentially in long-run equilibrium in 1984. Thus, the output vector and the capital stock level were sustainable, given the resource stock and market conditions, since no incentives for changes in the capital stock existed.

The hypothesis of long-run equilibrium is further supported by a comparison of the actual and optimal levels of *Z*. Departures between actual and optimal levels of a quasi-fixed factor can be tested by the significance of departures between its service and shadow prices (Kulatilaka, 1985). If the null hypothesis $W_Z = W_Z^*$ is not rejected, then the firm is in full equilibrium, i.e., $CU = 1$. Following Kulatilaka, we used a *t*-test to test the null hypothesis of full equilibrium, where the calculations are conditional on the observed sample means. The rental or market price of $Z$ ($W_Z$) used was the 1984 capital services price in units of gross registered tonnage of the vessel per trip. The values were derived from vessel acquisition prices obtained from confidential financial statements.[24] The shadow price of $Z$ ($W_Z^*$) was from equation (5), using the observed value of *Z*. The estimated *t*-statistic was 0.06, suggesting that effort was at its optimum, full-equilibrium level. Thus, the results of this test are consistent with the *CU* estimates obtained above.

### C. *The Effect of Output Quotas*

The effects of alternative output quotas on the cost- and profit-gap measures of *CU* were evaluated in the following manner. The estimated supply curves at the point of means were used to calculate the virtual price that would correspond to a given quota on output $Y_i$ at the individual vessel (firm) level for each fishing trip if all other product prices remain unchanged. Specifically, the virtual price $p_i$ corresponding to the quota-constrained output $y_i$ was solved from $y_i = Y_i^*(P_1, \ldots, P_{i-1}, p_i, P_{i+1}, \ldots, P_M; Z)$, where $Y_i^*(\cdot)$ is the estimated equation (4) for product *i*. The virtual price was then used to calculate $W_Z^*$ using equation (5). The new $CU^C$ and $CU^S$ measures were then calculated.

The effects of an output quota upon the cost- and profit-gap measures of *CU* are reported in table 4. All measures were evaluated at the observed sample mean, and quotas for each output were progressively set as 10%, 20%, and 30% reductions of the unconstrained sample mean production levels.[25] While the effects on the cost- and profit-gap measures are qualitatively similar, they are more pronounced for the profit-gap

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[24] The use of confidential financial data raises questions about replicability of the reported results by other researchers. While these data are not (and cannot be made) public, the authors could make arrangements for replicability if necessary.

TABLE 4.—ECONOMIC CAPACITY UTILIZATION MEASURES WITH OUTPUT QUOTAS

| Output Quota | | Dover Sole | Thorny-heads | Other Flatfish | Other Rockfish | All Others |
|---|---|---|---|---|---|---|
| 10% | Cost: | 0.5805 | 0.8091 | 1.0123 | 0.8814 | 1.0042 |
| | Profit: | 0.5331 | 0.7150 | 1.0264 | 0.8015 | 1.0088 |
| 20% | Cost: | 0.5688 | 0.7975 | 1.0123 | 0.8703 | 1.0040 |
| | Profit: | 0.5263 | 0.7028 | 1.0263 | 0.7869 | 1.0084 |
| 30% | Cost: | 0.5648 | 0.7946 | 1.0123 | 0.8641 | 1.0038 |
| | Profit: | 0.5239 | 0.6999 | 1.0262 | 0.7790 | 1.0081 |

Note: Calculated at observed sample mean for Eureka in the summer. Output quota corresponds to percentage reduction from mean production.

measure. This should not be surprising since $CU^S$ reflects the effect of the quota not only on shadow costs but also on revenue. This additional revenue effect reinforces the effect of the quotas on shadow costs, thereby increasing the investment incentives or disincentives beyond the levels implied by $CU^C$. This suggests that using the cost-gap measure of $CU$ for firms whose output levels are endogenous may understate the actual expansionary or contractionary forces of the regulation.

In terms of product-specific effects, as anticipated, the products with the highest shadow price elasticities, Dover sole and thornyheads, had the largest reductions in $CU$ in response to the quotas. Since the own-price product supply elasticities were highly inelastic, a comparatively large implicit price decrease was required to support each quota, contributing to the large reductions in $CU$ for Dover sole and thornyheads.

Output quotas in this industry are counted on to smooth production of overexploited resource stocks over the entire year, thereby maintaining year-round production, while not limiting the number of firms in the industry. Our results suggest that for most species quotas impose only minor implicit costs to firms in the form of implicit taxes and reductions in the firm's implicit marginal valuation of its quasi-fixed factor. For these outputs, quotas should not create disruptive capacity imbalances and disinvestment incentives. However, quotas on Dover sole and thornyheads are likely inadvertently to reduce rates of capacity utilization enough to induce disinvestment and ultimately exit of some firms from the industry. Since those firms exiting the industry may be among the more efficient, another form of regulation to reduce their production rate may be preferred.

## V. Summary

This paper has developed a methodology for using $CU$ measures to predict the expansionary or contractionary investment tendencies that would result from the imposition of input or output constraints such as quotas. The methodology uses the concept of virtual prices to translate a primal constraint into the corresponding dual constraint. This allows the effects of regulatory or other constraints to be examined ex ante, i.e., before they are imposed, so that concerns about these effects can be incorporated into policy design.

The results are presented using two alternative measures of capacity utilization for multiproduct, profit-maximizing firms. The two are based, respectively, on the cost and the profit gaps that result from being out of long-run equilibrium. Although the two measures provide equivalent qualitative information about the existence of investment incentives or disincentives, they differ in magnitude. To the extent that output adjustments are an important component of regulatory response, the profit-based measure, which incorporates endogenous output choices, seems to capture more accurately the magnitude of the incentives that would exist as a result of the regulatory constraint.

The methodology for predicting the effects of constraints on investment incentives or disincentives is illustrated through a case study of an open-access marine fishing industry on the Pacific Coast of the United States. The results indicate that output quotas may help allocate production over the entire year for most species when they face excessive exploitation, but that for two of the

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[25] The effects of an output quota were not evaluated for sablefish, because its own-price supply elasticity was negative (but statistically insignificant).

outputs, Dover sole and thornyheads, even seemingly generous quotas can create disinvestment pressures severe enough for firms to exit the industry. In this case, should reductions in industry capacity through disinvestment be desired, other forms of regulation and disinvestment incentives allowing efficient resource reallocation may be preferred.[26]

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[26] Individual transferable quotas are one possibility, since the most efficient firms can purchase the transferable production quotas while less efficient firms exit the industry. This approach maximizes social surplus and directly addresses the issue of property rights. License limitation is another alternative. The application of *CU* measures to this latter case is discussed by Segerson and Squires (1990a). For a discussion of the welfare effects of alternative policies used in fisheries management, see Waugh (1984).

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# The Role of the Neon Flying Squid, *Ommastrephes bartrami*, in the North Pacific Pelagic Food Web

by
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## I. ABSTRACT

Trophic relationships of neon flying squid, *Ommastrephes bartrami*, are examined during their summer occupation of waters within the Subarctic Frontal Zone and after their spawning migration south to subtropical waters. An examination of 174 stomachs from driftnet-caught *O. bartrami* near the Subarctic Boundary revealed many squid with empty stomachs and a high incidence of cannibalism. Squid with stomach contents fed exclusively on fishes (mainly micronektonic mesopelagic myctophids and stomiiformes) and other cephalopods. No significant difference was found between the diets (nor the degree of cannibalism) of *O. bartrami* when the stomach contents of squid taken near the Subarctic Boundary were compared with those of mature females collected during the winter in the subtropics.

Stomach contents are also described for blue sharks, *Prionace glauca*, captured by surface longlines in the North Pacific Transition Zone. Their most important diet items were myctophids, small gonatid squids, and *O. bartrami*. *Ommastrephes bartrami*, however, appeared important only among the larger sharks caught.

Results of these diet studies are discussed together with a review of pertinent literature to clarify the role of *O. bartrami* in the North Pacific pelagic food web.

## II. INTRODUCTION

Pelagic cephalopods are important both to commercial fisheries (Roper *et al.* 1984) and for their role within oceanic ecosystems. Epipelagic squids in particular are major components of oceanic food webs (Hedgepeth 1983). Considerable interest has been focused on the flying squid, *Ommastrephes bartrami*, an oceanic species found throughout temperate and subtropical regions worldwide and now the target of international driftnet fishing fleets (Roper *et al.* 1984; Murata 1990). Presently, little is known regarding the role of *O. bartrami* in the North Pacific pelagic food chain; such information, however, is an important consideration in any evaluation of the fishery's effects on the ecosystem.

The diets of *O. bartrami* and various fish species are being studied to understand trophic relationships in the central North Pacific ecosystem. Preliminary results of *O. bartrami* feeding habits during winter occupation of subtropical waters and their trophic relationship with swordfish, *Xiphias gladius*, were presented in Seki (in press). The intent of the present paper is threefold: to provide comparative information on the diet of *O. bartrami* taken near the Subarctic Boundary in the Subarctic Frontal Zone (SAFZ) during the summer fishing season; to present results on the feeding habits of a major predator, the blue shark (*Prionace glauca*), in the SAFZ; and to discuss these results, together with a review of pertinent literature, to clarify the role of *O. bartrami* in the North Pacific pelagic food web.

## III. MATERIALS AND METHODS

A total of 174 *O. bartrami* were collected from 18 sets of research gillnet during July-August 1990 aboard the research vessel *Shōyō maru* in waters of the SAFZ (Fig. 1). The gillnet was typically set around dusk and retrieved the ensuing morning. Although the gillnet was composed of varying mesh sizes (range = 48 to 157 mm stretch mesh), most of the flying squid were captured in 115 mm netting. Specifications of the fishing gear were described in Seki (1990). Squid ranging in dorsal mantle length from 163 to 490 mm ($\bar{L}$ = 322 mm, SD = 98.1) were frozen upon capture and returned to the laboratory for analysis. All of the squid were reproductively immature; 122 were females, 49 were males, and 3 were unsexed.

In the laboratory, frozen squid were thawed; stomachs were extracted and examined for the presence of food items. Empty stomachs were noted and discarded.

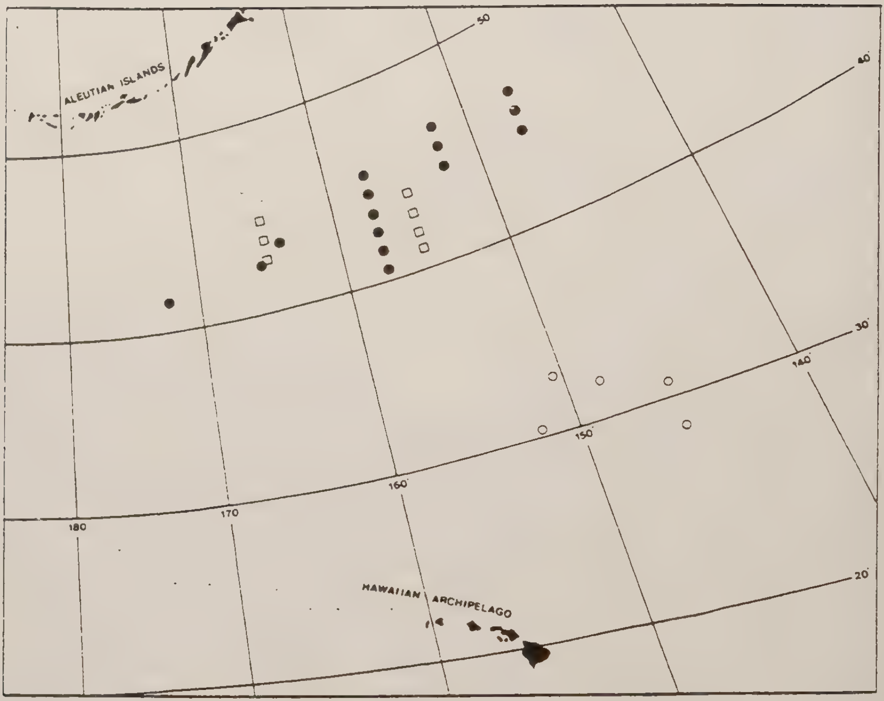

Fig. 1. Capture locations of *Ommastrephes bartrami* and *Prionace glauca* examined for analysis of stomach contents. Filled circles are summer *O. bartrami* collected by the research vessel *Shōyō maru*, open circles are winter *O. bartrami* collected by the research vessel *Shinriasu maru* (from Seki in press), and open squares are *P. glauca* collected via surface longlines by the NOAA ship *Townsend Cromwell*.

Stomachs with food items were fixed in a 10% phosphate-buffered formalin solution (Hunter 1985) and then transferred within 24 h to 50% isopropanol for preservation and storage. During processing, stomach contents were emptied into a 0.333 mm Nitex strainer, rinsed under running water, and sorted into identifiable groups. Sorted food items were blotted dry, and wet weights were measured to the nearest 0.1 g. Prey were identified to the lowest possible taxon; however, since stomach contents of cephalopods are normally minced into small fragments and are often well digested (Boucher-Rodoni *et al.* 1987), most of the food items were only classifiable into broad taxonomic categories. Cephalopod prey were identified primarily from suckers, hooks, beaks, and gladii; and fishes from vertebrae, teeth, epidermis, and otoliths. These stomach contents from squid captured in the SAFZ during summer were compared with similar feeding data from squid taken during the winter in subtropical waters (Fig. 1) (Seki in press), using the approach developed by Somerton (1991) to statistically detect seasonal differences in diets. Briefly, this approach (named DIETTEST) calculates variance and covariance of the gravimetric proportions for each prey group within each sample and subsequently measures between-sample differences utilizing Hotelling's $T^2$ statistic. For this test, *O. bartrami* stomach contents data were classified into three broad prey groups: fishes, squid, and cannibalized *O. bartrami*. The statistical significance of the measure was then determined from an empirical probability distribution of $T^2$ computed through randomization (Somerton 1991). Two thousand iterations of randomization were used on the present data set.

To provide additional information on the ecosystem dynamics of the region, food habit studies were also initiated on some fish species that are incidentally caught in the high seas driftnet fisheries targeting *O.*

*bartrami*. Included among these fishes is the blue shark, *Prionace glauca*. A total of 72 blue sharks 42.9-154.5 cm precaudal length (PCL), $\bar{L}$ = 73.6 cm PCL, SD = 32.9) were collected via surface longlines by the NOAA ship *Townsend Cromwell* within waters of the SAFZ during October 1989 (Fig. 1). Longlines were normally set just prior to sunrise and hauled about an hour after dawn. Upon capture, sharks were measured and stomachs extracted and examined for food items. Empty stomachs were noted and discarded; stomachs with food items were preserved in 10% formalin and returned to the laboratory for analysis. Laboratory procedures for the stomach analysis were similar to those described above for *O. bartrami*.

The index of relative importance (IRI) modified from Pinkas *et al.* (1971) was employed to assess the relative value of prey items. The IRI incorporates percentage by number (N), weight (W), and frequency of occurrence (F): IRI = %F(%N + %W).

## IV. RESULTS

Thirty-seven of the 174 *O. bartrami* stomachs examined contained prey. By weight, stomach contents ranged from 0.1 to 40.4 g ($\bar{W}$ = 15.7 g; SD = 12.1) and were composed entirely of cephalopods (51.8%) and fishes (48.2%) (Table 1).

Cephalopods occurred in 67.6% of the stomach samples. Although much of the cephalopod material was not identified, at least 56.9% by weight can be attributed to cannibalized *O. bartrami*. This cannibalism was found in 29.7% of the squid examined (i.e., those with some stomach contents) and represented 29.5% of the total aggregate weight of prey. Some teuthoid prey possessed several varieties of arm and tentacular hooks (probably from the families Gonatidae, Enoploteuthidae, and Onychoteuthidae) and were grouped together since they could be distinguished from the cannibalized material. These squid, normally well digested, made up 8.7% of the cephalopod food items by weight.

Fish remains were found in 62.2% of the stomachs and were typically in an advanced state of digestion. The identified fishes were composed of micronektonic myctophid and stomiiform fishes and the Pacific saury, *Cololabis saira*. As many as eight pairs of myctophid otoliths were recovered from a single stomach.

In the two-tailed probability tabulation, no significant difference was found between the summer and winter diets of *O. bartrami* ($T^2$ = 0.7775; 3 tests; $\alpha$ = 0.05). Comparative proportions of the major prey classes for the two seasons and localities are presented in Figure 2.

Thirty-two of the 72 blue shark stomachs examined contained some prey; stomach contents averaged 2.7 prey items (SD = 1.8) weighing 109.0 g (SD = 249.2) (Table 2). Fishes and cephalopods composed nearly all of the diet. Lanternfishes of the family Myctophidae (%IRI = 46.1), *O. bartrami* (%IRI = 29.3), and gonatid squids (%IRI = 14.8) were the most important dietary components based upon percent of IRI.

Table 1. Diet composition of 37 *Ommastrephes bartrami* captured in gillnets near the North Pacific Subarctic Boundary, July-August 1990.

| PREY SPECIES | WEIGHT (G) | PERCENT WEIGHT | FREQUENCY | PERCENT FREQUENCY |
|---|---|---|---|---|
| Cephalopods | | | | |
| *Ommastrephes bartrami* | 170.5 | 29.5 | 11 | 29.7 |
| Unidentified teuthoids (with hooks) | 26.0 | 4.5 | 4 | 10.8 |
| Unidentified Cephalopoda | 103.2 | 17.8 | 15 | 40.5 |
| Total | 299.7 | 51.8 | 25 | 67.6 |
| Fishes | | | | |
| Myctophidae | 47.5 | 8.2 | 8 | 21.6 |
| Stomiiformes | 13.3 | 2.3 | 2 | 5.4 |
| *Cololabis saira* | 33.7 | 5.8 | 1 | 2.7 |
| Unidentified fishes | 184.6 | 31.9 | 12 | 32.4 |
| Total | 279.1 | 48.2 | 23 | 62.2 |

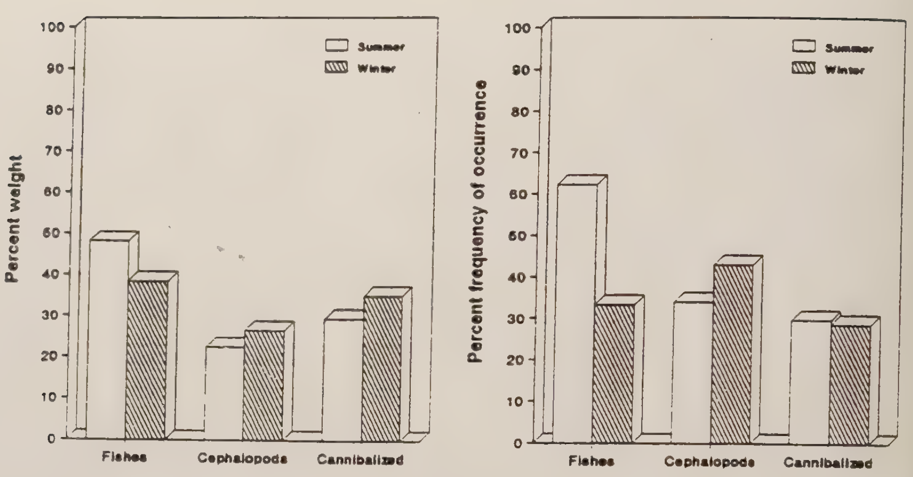

Fig. 2. Comparative proportions, by weight and by frequency of occurrence, of major prey classes in diets of *Ommastrephes bartrami* captured during summer in the Subarctic Frontal Zone (n = 37) and during winter in the subtropics (n = 42).

Table 2. Stomach contents of blue shark, *Prionace glauca* (n = 32), captured by surface longlines in the Subarctic Frontal Zone (IRI = index of relative importance).

| PREY ITEMS | NO. | % | WEIGHT | % | FREQUENCY | % | IRI | % |
|---|---|---|---|---|---|---|---|---|
| | | | | **Fishes** | | | | |
| Sternoptychidae | | | | | | | | |
| *Argyropelecussp.* | 1 | 1.15 | 2.9 | 0.08 | 1 | 3.13 | 3.85 | 0.1 |
| Myctophidae | 34 | 39.08 | 60.0 | 1.73 | 17 | 53.13 | 2167.93 | 46.1 |
| Alepisauridae | | | | | | | | |
| *Alepisaurus ferox* | 1 | 1.15 | 240.3 | 6.92 | 1 | 3.13 | 25.22 | 0.5 |
| Bramidae | | | | | | | | |
| *Brama japonica* | 2 | 2.30 | 418.4 | 2.05 | 2 | 6.25 | 89.67 | 1.9 |
| Pentacerotidae | | | | | | | | |
| *Pseudopentaceros wheeleri* | 1 | 1.15 | 226.4 | 6.52 | 1 | 3.13 | 23.96 | 0.5 |
| Gempylidae | 1 | 1.15 | 106.4 | 3.06 | 1 | 3.13 | 13.17 | 0.3 |
| Unidentified fishes | 6 | 6.90 | 283.2 | 8.15 | 4 | 12.50 | 188.14 | 4.0 |
| | | | | **Cephalopods** | | | | |
| Ommastrephidae | | | | | | | | |
| *Ommastrephes bartrami* | 8 | 9.20 | 1865.8 | 53.73 | 7 | 21.88 | 1376.41 | 29.3 |
| Onychoteuthidae | 3 | 3.45 | 37.3 | 1.07 | 3 | 9.38 | 42.40 | 0.9 |
| Gonatidae | 24 | 27.59 | 6.1 | 0.18 | 8 | 25.00 | 694.05 | 14.8 |
| Ocythoidae | | | | | | | | |
| *Ocythoe tuberculata* | 1 | 1.15 | 209.4 | 6.03 | 1 | 3.13 | 22.43 | 0.5 |
| Unidentified squid | 3 | 3.45 | 14.3 | 0.41 | 3 | 9.38 | 36.19 | 0.8 |
| | | | | **Others** | | | | |
| Lophogastridae | | | | | | | | |
| *Gnathophausia* sp. | 2 | 2.30 | 2.3 | 0.07 | 2 | 6.25 | 14.81 | 0.3 |
| Total | 87 | 100.00 | 3472.8 | 100.00 | -- | --- | 4698.23 | 100.0 |

Figure 3 presents the diet composition of blue sharks when grouped into two size modes: ≤65 cm and >65 cm PCL. Twelve of the 25 stomachs from sharks >65 cm PCL contained food, including all of the *O. bartrami* recorded as prey in this study. Forty-seven of the sharks were ≤65 cm PCL; 27 had empty stomachs. Micronektonic myctophids and small gonatids dominated prey consumed by the smaller sharks.

## V. DISCUSSION

In the North Pacific Ocean, *O. bartrami* are generally distributed between 25° and 50°N latitude (Roper *et al.* 1984), and exhibit extensive seasonal horizontal and diel vertical migrations. During late spring, *O. bartrami* migrate from presumed winter spawning grounds in the Subtropical Domain northward to feeding grounds near the Subarctic Boundary in the SAFZ. Reverse migration occurs during autumn through early winter (Araya 1983; Gong 1985; Murata *et al.* 1988; Murata 1990). Recent studies employing ultrasonic telemetry have revealed that *O. bartrami* occupy waters within 100 m of the surface at night, vertically migrating to waters below 400 m (often to depths of >700 m) where they remain during the day (Nakamura in press). The wide-ranging habitat of the species would seem to make *O. bartrami* highly susceptible to numerous predators, and consequently, their trophic relationships are quite complex. Nevertheless, understanding the role of *O. bartrami* in the North Pacific pelagic food web is critical in the evaluation of the ecosystem effects of the high seas driftnet fishery.

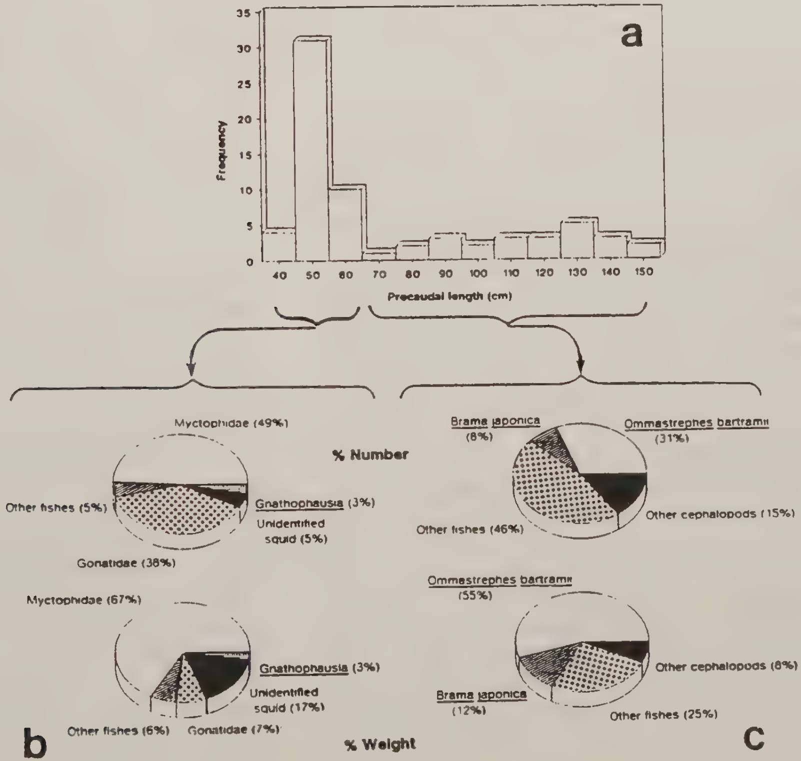

Fig. 3. Length frequency (a) and comparison of diet composition in blue sharks, *Prionace glauca*, ≤65 cm precaudal length (b) and >65 cm PCL (c) taken by surface longlines near the Subarctic Boundary.

*Ommastrephes bartrami*, like most teuthoids in general, are nonselective, active carnivores (Boucher-Rodoni *et al.* 1987) and, in the present study, fed totally on fishes and squid. Jig-caught *O. bartrami* in the western North Pacific also fed primarily on fishes and secondarily on squid (Naito *et al.* 1977; Araya 1983). Fishes included lanternfishes and small pelagics (e.g., sardines, juvenile mackerel, and saury); identified squids were the enoploteuthin *Watasenia scintillans*; boreal clubhook squid, *Onychoteuthis borealijaponica*; and cannibalized *O. bartrami*. Crustaceans, such as euphausiids and hyperiid amphipods, were found occasionally among flying squid stomach contents in these temperate studies, but this result was attributed to the inclusion of smaller, immature squid that tend to feed more readily on plankton (Murata 1990). Fishes and cephalopods were the predominant prey of large female *O. bartrami* taken in subtropical central North Pacific waters (Seki 1991). Most of the cephalopod prey were attributed to cannibalism; however, the possibility that the cannibalism was an artifact induced by sampling techniques was suggested. In the present study, no significant difference was found between the diets (nor the degree of cannibalism) of squid taken in the summer in the SAFZ and mature female squid taken during winter in the subtropics. The inability to distinguish more of the prey into lower taxonomic levels limits the testing of qualitative differences in diet.

The limited information presented here on blue shark diets in the central North Pacific corroborates the results of prior diet studies. Blue sharks are known to feed indiscriminately on numerous species of small pelagic fishes and cephalopods (Strasburg 1958; Tricas 1979; Compagno 1984b). Overall, blue sharks in the present study also fed almost totally on small fishes and cephalopods. However, forage composition differed markedly for sharks ≤65 cm PCL as compared to those >65 cm PCL. Certain species were eaten by only larger sharks: *O. bartrami* and species such as Pacific pomfret, *Brama japonica*; pelagic armorhead, *Pseudopentaceros wheeleri*; and the pelagic octopus, *Ocythoe tuberculata*, which frequents surface waters. By comparison, small micronektonic lanternfishes and gonatid squids dominated the diet in sharks ≤65 cm PCL. Most of the prey species undergo diel vertical migrations, occupying surface waters at night. As nocturnally active predators (Tricas 1979), the blue sharks likely fed on most of the prey species during this time.

Few other fishes have been identified as predators of *O. bartrami* and none while the squid occupy SAFZ waters. Brodeur (1988) reviewed available trophic information for the dominant epipelagic fishes of the North Pacific Subarctic and Transition Zones. Abundant species such as *B. japonica* and albacore, *Thunnus alalunga*, were intermediate level predators feeding on micronektonic epi- and mesopelagic fishes, crustaceans, and cephalopods. Apex predatory fishes in the SAFZ were primarily sharks, including the blue shark; salmon shark, *Lamna ditropis*; and mako shark, *Isurus oxyrinchus*. Salmon sharks are not known to feed on cephalopods (Brodeur 1988); mako sharks feed opportunistically on available nekton (Compagno 1984a).

It is worth noting that, although diets of many of the pertinent species encountered in and potentially affected by the squid driftnet fishery have been studied, results are often not directly applicable to current assessments of *O. bartrami* trophic interactions. Nearly all of these past studies were conducted in geographical areas where *O. bartrami* are not common. Nevertheless, likely predators of *O. bartrami* are inferred on the basis of similar prey preferences and current knowledge of the species' distribution.

In subtropical waters, predators of *O. bartrami* include tunas, billfishes, and resident shark species. Perhaps the most notable of these predators is *X. gladius*, the target of a recently developed surface longline fishery. Ommastrephids, including large, mature *O. bartrami*, comprised most of the squid sampled from stomachs of *X. gladius* captured in large mesh driftnets (Seki in press). Predator-prey relationships between aggregations of winter-migrating *O. bartrami* and the seasonally abundant *X. gladius* have been suggested as possible impetuses for the fishery. Other billfishes–including blue marlin, *Makaira mazara*; striped marlin, *Tetrapturus audax*; and shortnose spearfish, *T. angustirostris*–reportedly feed commonly on ommastrephid squid (Nakamura 1985). Similarly, tuna species such as yellowfin tuna, *Thunnus albacares*; bigeye tuna, *T. obesus*; bluefin tuna, *T. thynnus*; and skipjack tuna, *Katsuwonus pelamis*, are also known to feed heavily on squid (Reintjes and King 1953; King and Ikehara 1956; Pinkas *et al.* 1971; Matsumoto 1984) and are likely predators of particularly the young *O. bartrami*.

Most information available on the interrelationships of *O. bartrami* and marine mammals can be found in an extensive review of the role of marine mammals in the oceanic food web of the eastern subarctic Pacific by Kajimura and Loughlin (1988). Basically, 11 marine mammal species (9 toothed cetaceans and 2 pinnipeds) have been identified to feed in oceanic areas near the Subarctic Boundary where encounters with *O. bartrami* are likely. Cetaceans include the sperm whale, *Physeter macrocephalus*; the short-finned pilot whale, *Globicephala macrorhynchus*; Dall's porpoise, *Phocoenoides dalli*; the Pacific whitesided dolphin, *Lagen-*

*orhynchus obliquidens*; Risso's dolphin, *Grampus griseus*; the northern right whale dolphin, *Lissodelphis borealis*; Baird's beaked whale, *Berardius bairdii*; Cuvier's beaked whale, *Ziphius cavirostris*; and the Stejneger's beaked whale, *Mesoplodon stejnegeri*. In warmer waters of the SAFZ and subtropics, other cetaceans that potentially feed on *O. bartrami* include the pygmy sperm whale, *Kogia breviceps*; dwarf sperm whale, *K. simus*; common dolphin, *Delphinus delphis*; and striped dolphin, *Stenella coeruleoalba*. Although the above-mentioned toothed cetaceans appear to favor oceanic squid as prey, only sperm whales reportedly have specifically fed on *O. bartrami* (Okutani *et al.* 1976; Okutani and Satake 1978; Kawakami 1980; Fiscus 1982). Among pinnipeds, remains of *O. bartrami* have been found in lavage studies of the northern elephant seal, *Mirounga angustirostris* (Antonelis *et al.* in press). Northern fur seals, *Callorhinus ursinus*, studied in neritic environments are also known to favor oceanic squid (Kajimura 1984).

The distribution and feeding ecology of pelagic seabirds in the subarctic Pacific have been summarized in Sanger and Ainley (1988). Forty species reportedly occur in the region (21 commonly); most of them are small Procellariiformes (i.e., shearwaters and petrels). Not surprisingly (since adult squid outweigh the birds), none of the bird species has been found to prey on *O. bartrami*. In the subtropics, however, juvenile *O. bartrami* are seasonally eaten by red-footed boobies, *Sula sula* (Seki and Harrison 1989), and many of the unidentified young ommastrephids found in winter-collected regurgitations from other seabird species in the Northwestern Hawaiian Islands also were very likely *O. bartrami* (Harrison *et al.* 1983).

A schematic representation of direct predator-prey relationships involving *O. bartrami*, based upon information summarized in the present paper, is illustrated in Figure 4. Relationships between individual prey and predator groups were not considered, and no attempt was made at estimating annual biomass, production, or consumption rates for the components. Estimation of these input parameters in future studies is critical for the development of an ecosystem model.

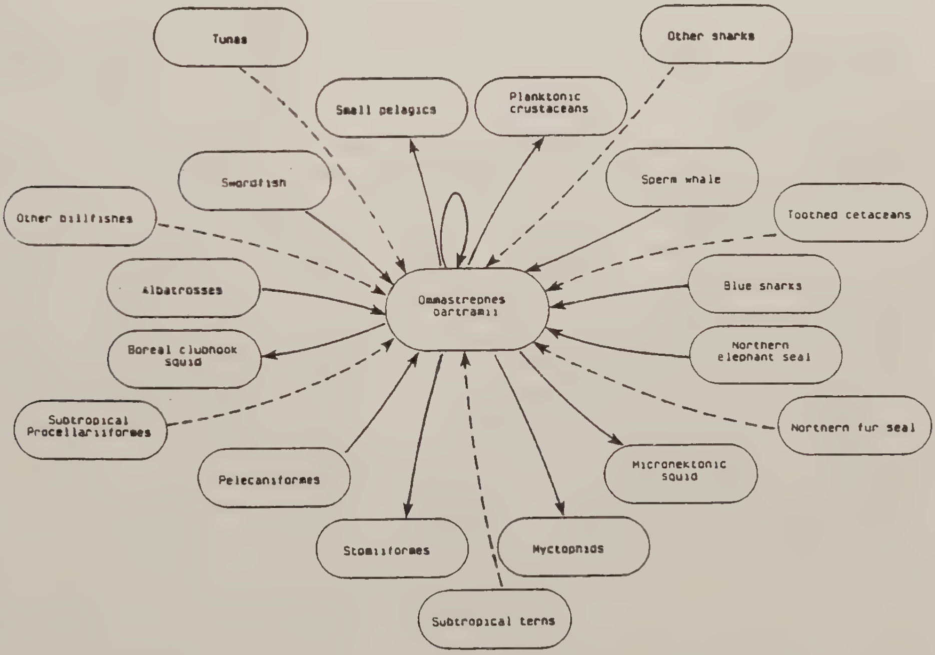
Tunas
Other sharks
Small pelagics
Planktonic crustaceans
Swordfish
Sperm whale
Other billfishes
Toothed cetaceans
Albatrosses
Ommastrephes bartramii
Blue sharks
Boreal clubhook squid
Northern elephant seal
Subtropical Procellariiformes
Northern fur seal
Pelecaniformes
Micronektonic squid
Stomiiformes
Myctophids
Subtropical terns

Fig. 4. Simplified schematic representation of *Ommastrephes bartrami* predator-prey relationships in the central North Pacific Ocean. Solid lines indicate known relationships; dashed lines are likely predators.

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# Trophic Relationships of *Ommastrephes bartramii* During Winter Migrations to Subtropical Waters North of the Hawaiian Islands

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**Abstract:** *Ommastrephes bartramii*, occupy waters in the North Pacific near the Subarctic Boundary during summer and fall where they are targeted by international driftnet fishing fleets. During the winter, *O. bartramii* migrate south to spawn in subtropical waters probably between 25° and 35°N latitude. Diet and trophic relationships were examined for *O. bartramii* during the winter occupation of these subtropical waters. Food composition was determined for stomachs from 42 large (48–57 cm mantle length), mature female *O. bartramii* captured by large (180 mm) mesh driftnet (ōme ami) during 12–19 February 1991. The bulk of the diet was composed of cephalopods (60.5%) and micronektonic fishes (37.7%); cannibalism was common. The relationship between winter-migrating *O. bartramii* and the recently developed swordfish, *Xiphias gladius*, longline fishery is also discussed. Squids found among swordfish stomach contents included adult *O. bartramii*, *Thysanoteuthis rhombus*, and *Sthenoteuthis oualaniensis*.

## Introduction

*Ommastrephes bartramii*, are broadly distributed in temperate and subtropical regions worldwide (Roper *et al.*, 1984). In the North Pacific, *O. bartramii* generally are known to occur between 25° and 50°N latitude. During summer and fall, *O. bartramii* occupy waters near the Subarctic Boundary (primarily between 36° and 46°N latitude), where they are targeted by international driftnet fishing fleets. With the onset of winter, these squid are thought to undergo extensive seasonal migration from these "feeding" grounds to the subtropics (ca. 25° and 35°N latitude) where presumed spawning occurs from late January through May (Araya, 1983; Gong, 1985; Murata *et al.*, 1988; Murata, 1990). Apparently, within a few months of hatching, juvenile *O. bartramii* begin a spring-summer migration northward to the region of the Subarctic Boundary, where they rapidly grow and remain until late fall when the return southern migration begins (Murata, 1990).

Information on the distribution of mature females (Nakamura, 1988) and the capture of the species' rhynchoteuthion paralarvae (Okutani, 1968) indicate that spawning grounds for *O. bartramii* exist west of 165°E longitude between 26° and 35°N latitude. Similarly, Young and Hirota (1990) and Hayase (1990) have reported captures of *O. bartramii* paralarvae along the Hawaiian Ridge during February–May. Little else, however, is known about the distribution, ecology, and life history of these squid during their winter and spring occupation of subtropical waters.

As a surface longline fishery targeting swordfish, *Xiphias gladius*, developed in the waters north of the Hawaiian Archipelago, swordfish landings in Hawaii increased from just 23,000 kg in 1988 to approximately 300,000 kg in 1989 and exceeded 1,000 metric tons in 1990. The fishery normally operates in the waters north of the Hawaiian Archipelago between 25° and 40°N latitude; peak effort and catches occur during March through May (NMFS, unpubl. data). Interestingly, the timing of the fishery coincides with the winter migration of *O. bartramii* to the subtropics. Since swordfish are recognized as major predators of squid (and ommastrephids in particular), possible predator-prey interrelationships exist between the aggregations of winter-migrating *O. bartramii* and the abundant swordfish. Swordfish stomach contents were investigated to examine these relationships.

In this paper, trophic relationships of winter-migrating adult *O. bartramii* are examined. Information is presented on the diet of these subtropical resident squid and their predator-prey relationship with swordfish.

## Materials and Methods

Stomachs from 42 large (48–57 cm mantle length (ML)), mature female *O. bartramii* captured by 180 mm stretched mesh surface gillnet (ōme ami) were extracted and frozen aboard the research vessel *Shin-Riasu maru* on 12–19 February 1991 in the general vicinity of 30°N latitude, 150°W longitude (Fig. 1). Squid were sampled from five gillnet sets which were deployed during 1500–1600h and normally retrieved during 0000–0300h. One gillnet set was retrieved at 0700–1035h the ensuing morning.

In the laboratory, the frozen stomachs were thawed and the contents removed for quick fixing in a 10% phosphate buffered formalin solution (Hunter, 1985). After 24h, stomach contents were transferred to 50% isopropanol for preservation and storage. During processing, stomach contents were emptied into a 333 μm Nitex strainer, rinsed under running water, and sorted into identifiable groups. Sorted food items were blotted dry, and wet weights were measured to the nearest 0.1g. Prey were identified to the lowest possible taxon; however, since stomach contents of cephalopods are normally minced into small fragments and are often well digested (Boucher-Rodoni *et al.*, 1987), most of the food items were only classifiable into broad systematic categories. Cephalopod prey were identified primarily from suckers, hooks, beaks, and gladii; and fishes from vertebrae, teeth, epidermis, and otoliths.

To examine the predator-prey relationship between adult *O. bartramii* and *X. gladius*, squid from the stomachs of 22 swordfish caught in subtropical waters in the vicinity and north of the Hawaiian Archipelago were opportunistically collected and frozen during 1989 through 1991. Nineteen of the swordfish were captured by surface longline aboard the NOAA ship *Townsend Cromwell* or on commercial fishing vessels; the remaining three swordfish were caught in ōme ami driftnet operations aboard the *Shin-Riasu Maru* (Fig. 1).

In the laboratory, individual squid from swordfish stomachs were thawed and identified to the

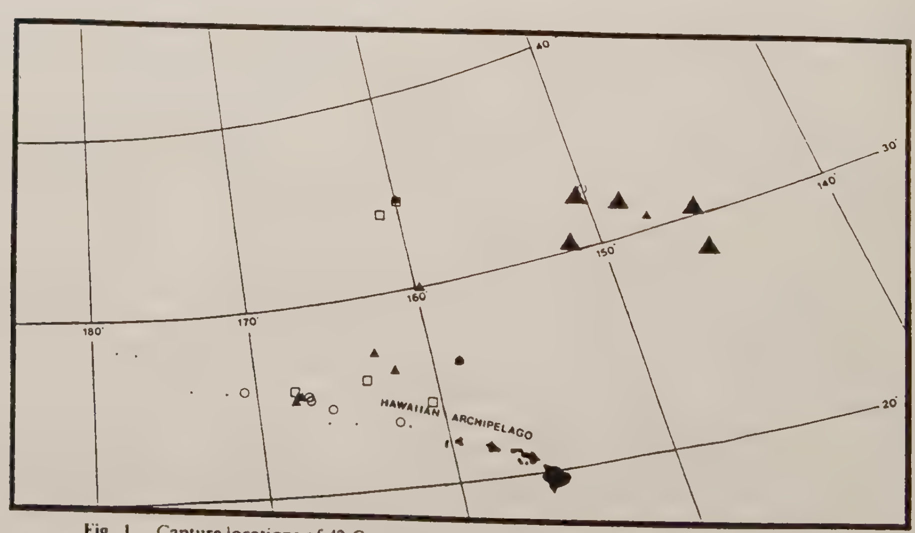

Fig. 1. Capture locations of 42 *Ommastrephes bartramii* and 22 *Xiphias gladius* in waters north of the Hawaiian Archipelago.
▲: *O. bartramii* collected from the stomachs of *X. gladius*
○ : *Thysanoteuthis rhombus* collected from the stomachs of *X. gladius*
□ : *Sthenoteuthis oualaniensis* collected from the stomachs of *X. gladius*
▲ : *O. bartramii* collected from ōme ami gillnet operations aboard the *Shin-Riasu Maru*

lowest possible taxon using the methodology similar to that described by Hess and Toll (1981). Briefly, squid identifications were based on a composite of characters such as mantle musculature, shape of mantle locking mechanism, gladius and beak morphology, statoliths, and light organs. All of the long-lines from which samples were obtained were baited with *Illex* sp. (all examined were *I. argentinus*), which were excluded from the analysis when found among the stomach contents.

The MLs were obtained for squid that had undergone minimal digestion; gladius length was interpreted as ML for others. The ML estimations for squid digested beyond reliable length measurements (particularly *Sthenoteuthis oualaniensis*) were based upon the relationship between rostral length of the lower beak (LRL) and ML (Wolfe, 1982).

## Results

All 42 of the examined *O. bartramii* stomachs contained prey; some samples (13), however, contained $<1.0$g total prey weight and could be considered empty. By weight, stomach contents ranged from 0.1 to 220.0g ($\bar{x} = 16.3$g; SD = 34.4) and were composed primarily of cephalopods (60.5%) and fishes (37.7%) (Table 1).

Cephalopods occurred in 71.4% of the stomach samples. Thus far, only squid of the family Ommastrephidae have been positively identified—a reflection of the unusually fresh condition of the prey which facilitated identification. Cannibalized *O. bartramii* were determined to be present in at least 14.3% of the stomachs and by weight represented 77.0% of the ommastrephid and 32.9% of the overall cephalopod material consumed. Non-ommastrephid squid normally were well digested and possessed several varieties of arm and tentacular hooks. These were probably from the families Gonatidae, Onychoteuthidae, and Enoploteuthidae.

Fish remains were found in 33.3% of the stomachs and were typically in advanced stages of digestion. Vertebrae morphology and pieces of epidermis suggested that most of the fishes were either micronektonic myctophids or stomiiforms. A single pair of otoliths was identified as belonging to *Myctophum* sp.

Miscellaneous prey such as pyrosomes, crustaceans, barnacles (suborder Lepadomorpha), undigestible plastics (monofilament), and general unidentifiable remains also were found among the stomach contents. These items together made up only 1.8% of the total aggregate weight.

Large teuthoids of the families Ommastrephidae (*O. bartramii* and *S. oualaniensis*) and Thysanoteuthidae (*Thysanoteuthis rhombus*) composed the cephalopod fauna collected from sword-

**Table 1.** Diet composition of 42 mature female *Ommastrephes bartramii* from the subtropical central North Pacific Ocean, 12–19 February 1991.

| Prey species | Weight (g) | Percent weight | Frequency | Percent frequency |
|---|---|---|---|---|
| Cephalopods | | | | |
| *Ommastrephes bartramii* | 136.3 | 19.9 | 6 | 14.3 |
| Unidentified Ommastrephidae | 67.2 | 9.8 | 4 | 9.5 |
| Non-Ommastrephidae (i.e. teuthoids with hooks) | 58.0 | 8.5 | 7 | 16.7 |
| Unidentified Cephalopoda | 152.9 | 22.3 | 13 | 30.9 |
| Total Cephalopoda | 414.4 | 60.5 | 30 | 71.4 |
| Fishes | | | | |
| *Myctophum* sp. | 17.9 | 2.6 | 1 | 2.4 |
| Unidentified fishes | 240.0 | 35.1 | 13 | 30.9 |
| Total fishes | 257.9 | 37.7 | 14 | 33.3 |
| Others | | | | |
| Barnacles (Suborder Lepadomorpha) | 3.2 | 0.5 | 1 | 2.4 |
| Crustacea | 0.8 | 0.1 | 2 | 4.8 |
| Pyrosomatidae | 0.3 | <0.1 | 1 | 2.4 |
| Unidentified remains | 6.7 | 1.0 | 11 | 26.1 |
| Plastic (monofilament) | 1.1 | 0.2 | 2 | 4.8 |
| Total others | 12.1 | 1.8 | 17 | 40.5 |
| Totals | 684.5 | 100.0 | 122 | — |

**Table 2.** Number, percent frequency of occurrence, estimated range of mantle lengths (ML), and months of capture of squids collected from the stomachs of 22 swordfish, *Xiphias gladius*, in the subtropical central North Pacific Ocean, 1989–1991.

| Species | No. | Percent frequency | ML (mm) | Months of capture |
|---|---|---|---|---|
| *Ommastrephes bartramii* | 9 | 40.9 | 357–495 | Jan, Feb, June, Sept, Oct |
| *Sthenoteuthis oualaniensis* | 5 | 18.3 | 187–334 | Jan, July, Aug, Sept |
| *Thysanoteuthis rhombus* | 7 | 31.8 | 330* | Jan, Feb, June, Nov, Dec |
| Unidentified ommastrephid | 3 | 13.6 | 210 | Jan, Feb, Aug |

* Most specimens too digested to obtain reasonable ML estimations; good relationship between beak length and ML for *Thysanoteuthis rhombus* not available.

fish stomachs in the subtropical central North Pacific Ocean (Table 2). Nine *O. bartramii* ranged in estimated ML from 357 to 495 mm ($\bar{x}$ = 437.7, SD = 49.6); five were females possessing mature eggs in the oviducts. Only one of the *T. rhombus* was sufficiently intact to obtain an ML measurement (330 mm). Although both upper and lower beaks were recovered from all of the *T. rhombus* individuals, a good relationship between beak morphometrics and ML does not exist at the present time.

One specimen of *O. bartramii* taken from the swordfish stomachs possessed an intact stomach which unfortunately was empty.

## Discussion

In this study, cephalopods and fishes dominated the prey composition in diets of the large adult female *O. bartramii* examined while crustaceans were virtually nonexistent. These results suggest that the winter diet of *O. bartramii* in the subtropics is similar to that reported for the species in more temperate regions. Naito *et al.* (1977) and Araya (1983) examined the stomach contents of jig-caught *O. bartramii* in North Pacific waters adjacent to Japan and described the species as primarily piscivorous (myctophids composed the bulk of fishes eaten) and cannibalistic. In addition to its own species, cephalopod prey included the enoploteuthid *Watasenia scintillans*. Crustaceans were more prevalent among the stomach contents of *O. bartramii* in these temperate studies, but this was attributed to the inclusion of smaller immature squid that tend to feed more readily on plankton (Murata, 1990).

The natural feeding habits of *O. bartramii*, however, are difficult to assess because existing methods of squid fishing are inadequate for obtaining unbiased samples for diet studies. Most feeding studies of oceanic squid historically have obtained samples through the use of jigs after attraction of the animals with high-intensity lamps. Because fishing with lights also attracts and aggregates smaller, photopositive, vertically migrating micronekton, an artificially rich feeding environment with abnormal illumination is created. Naturally, feeding activity is increased, and ultimately stomach content analysis is affected by artifacts of the sampling. To circumvent potential biases that may have been created from the use of lights and jigs in sampling, the present study used only squid sampled with drift gillnets. Off Australia, Dunning and Brandt (1985) conducted the only published feeding study on *O. bartramii* captured with gillnets. In an examination of 138 individuals, 67% of the stomachs were found empty. Fishes and cephalopods composed most of diet, although pteropods also were common. Moreover, no evidence of cannibalism was presented.

Cannibalism is a commonly reported phenomenon among some schooling squid species and especially so among ommastrephids (Nixon, 1987) and appeared to be common among *O. bartramii* in the present study. Some authors (Maurer and Bowman, 1985) have suggested that cannibalism indicates a lack of other suitable prey in the area. Field observations, however, support the notion that much of the reported cannibalism may be induced by the sampling technique (Breiby and Jobling, 1985). *Sthenoteuthis oualaniensis* has been observed in Hawaiian waters to prey upon its own species when injured animals were being retrieved during jigging operations (R.E. Young, pers. commun., June 1991). Not surprisingly, freshly cannibalized squid could often be found in stomachs of those captured and examined (R.F. Harman, pers. commun., June 1991). Undoubtedly, this is a common behavior among ommastrephids around fishing lights. Cannibalism was also unexpectedly observed for *O. bartramii* during high seas squid driftnet fishing operations conducted aboard the research vessel *Shōyō-Maru* operating in the vicinity of the Subarctic Boundary in July 1990. Remains of partially cannibalized *O. bartramii* commonly were entangled in retrieved nets and also were identified in stomachs casually examined during shipboard processing. Apparently, squid were attacking others that had been caught by the nets during fishing. The fresh condition of cannibalized squid found in the stomachs during the present study suggests that this too may be an induced artifact of sampling rather than a natural feeding behavior.

Cephalopods comprised all of the fresh material in the stomachs; the majority were ommastrephids and specifically *O. bartramii.* Normally these items included only portions of an individual, such as a fraction of an arm with suckers or minced mantle often with the epidermis intact. Breiby and Jobling (1985) suggested using only the most digested stomachs in squid feeding studies that employ gravimetric analysis. Dietary analysis using gravimetric (or volumetric) methods was found to treat recently consumed prey as the most important components (i.e., emphasized the importance of cannibalism). If fresh material were to be excluded from this analysis, fishes and cephalopods would still dominate the food composition; however, the diet would appear to be considerably more piscivorous (Fig. 2). Ommastrephids would still represent 38.0% of the cephalopods eaten, but none of the remaining material has been verified as *O. bartramii.* The average weight of stomach contents would fall to 10.6g (SD = 21.2), and 16.7% of the individuals would now be classified as empty. Further study is required to determine whether the cannibalism exhibited among *O. bartramii* is induced by sampling techniques or is, in part, a function of natural feeding behavior and survival.

The limited results presented here for the central North Pacific corroborate the findings of prior swordfish feeding studies conducted in other areas. Swordfish appear to demonstrate a clear predilection for teuthoids as prey (Toll and Hess, 1981), and among squid species, ommastrephids in particular are preferred. This is exemplified by the predation on species of *Illex* in the North Atlantic (Scott and Tibbo, 1968; Stillwell and Kohler, 1985) and off Portugal (Moreira, 1990), on *Illex* and *Ommastrephes* off South Florida (Toll and Hess, 1981), and on *Dosidicus gigas* in the eastern Pacific (DeSylva, 1962). Similarly, *O. bartramii* and *S. oualaniensis,* the most abundant, large ommastrephid species in the central Pacific, were among common prey.

Swordfish undergo diel vertical migrations, swimming deep during the day (to about 100m) (Carey and Robison, 1981) and occupying near-surface epipelagic waters at night where they feed (Palko et al., 1981; Toll and Hess, 1981). Similarly, *O. bartramii* inhabit near-surface waters at night, as evidenced by their susceptibility to surface gillnets, and diurnally occupy depths greater than 400m (Nakamura, this volume). In addition, swordfish are thought to exploit schools of prey as opposed to individuals (Scott and Tibbo, 1968). *Ommastrephes bartramii,* like many teuthoids, commonly aggregate for feeding (Clarke, 1966). With these convergent behaviors, swordfish predation on *O. bartramii* (or any ommastrephid species) would seem likely.

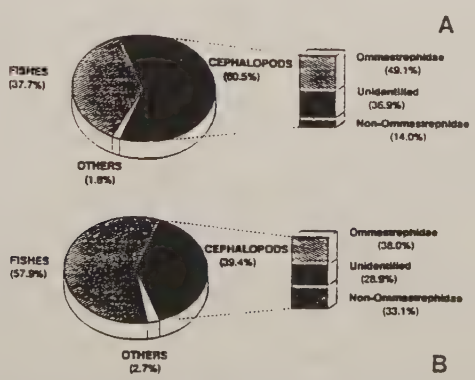

**Fig. 2.** Comparative proportions by weight of major prey classes in diets of *Ommastrephes bartramii* with fresh (recently consumed) material (A) included in and (B) excluded from the analysis.

Many of the squids sampled from swordfish stomachs were mature, suggesting that swordfish may indeed be feeding on concentrations of spawning *O. bartramii*. Additional data of this type may aid in delineating spawning grounds and season in the central North Pacific for this species. Further study is needed to understand the role of *O. bartramii* both as predator and prey in the ecosystem of the subtropical North Pacific. Sampling constraints that result in cannibalism will continue to hinder qualitative as well as quantitative assessments of diet until new capture methodologies are developed.

## Acknowledgements

The Fisheries Agency of Japan and the officers and crew of the R/V *Shin-Riasu Maru* provided the opportunity to sample aboard their research vessel. Specimens used in this study were also collected and furnished by R. Dollar, R. Ito, K. Kawamoto, B. Mounier, J. Sicina, and the NOAA ship *Townsend Cromwell* cruise TC-91-01. K.A. Bigelow, E.D. DeMartini, R.F. Harman, and R.E. Young provided helpful suggestions on earlier drafts of the manuscript. It is a pleasure to thank all of these people.

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9383

# Aspects of the Life History and Ecology of the Pacific Pomfret *Brama japonica* During Winter Occupation of the Subtropical Frontal Zone

by

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## I. ABSTRACT

One of the most widely distributed and abundant nektonic animals in the epipelagic North Pacific Ocean is the Pacific pomfret *Brama japonica*. We present various ecological and life history aspects of *B. japonica* based on 148 larval and juvenile specimens collected with a midwater trawl at 8 locations north of the Hawaiian Islands near the Subtropical Frontal Zone (STFZ). Most *B. japonica* were caught within the mixed layer in water temperatures of 17.5°-19.8°C; their distribution was limited to the south by the 21°C isotherm. Satellite data depicting the location of the STFZ, in conjunction with catch data, indicate that larval and juvenile *B. japonica* were typically distributed to the north of the Subtropical Front. Ages and growth rates of 32 larvae and juveniles were determined through analysis of otolith microstructures: Estimated ages were 1-2 months, and estimated growth rate was 0.353 mm $d^{-1}$ for 11-24 mm standard length fish and hatching dates based on back-calculated age estimates were 2-30 January 1991. An examination of the feeding habits of pomfrets caught by driftnet near the STFZ revealed that most of the stomachs were empty; hyperiid amphipods along with other unidentified crustaceans were predominant in the stomachs that contained prey.

## II. INTRODUCTION

Pacific pomfret *Brama japonica* are widely distributed in oceanic waters across the North Pacific approximately between 25° and 50°N latitude (Shimazaki and Nakamura 1981). As a predominant component of the incidental bycatch of the high seas squid driftnet fishery (second only to the target species in total biomass; INPFC 1991), *B. japonica* are considered to be among fishes with low economic value and are generally discarded when caught. Historically, *B. japonica* have drawn attention as an underutilized but promising fishery resource (Hitz and French 1965; Barnett and Teeny 1981).

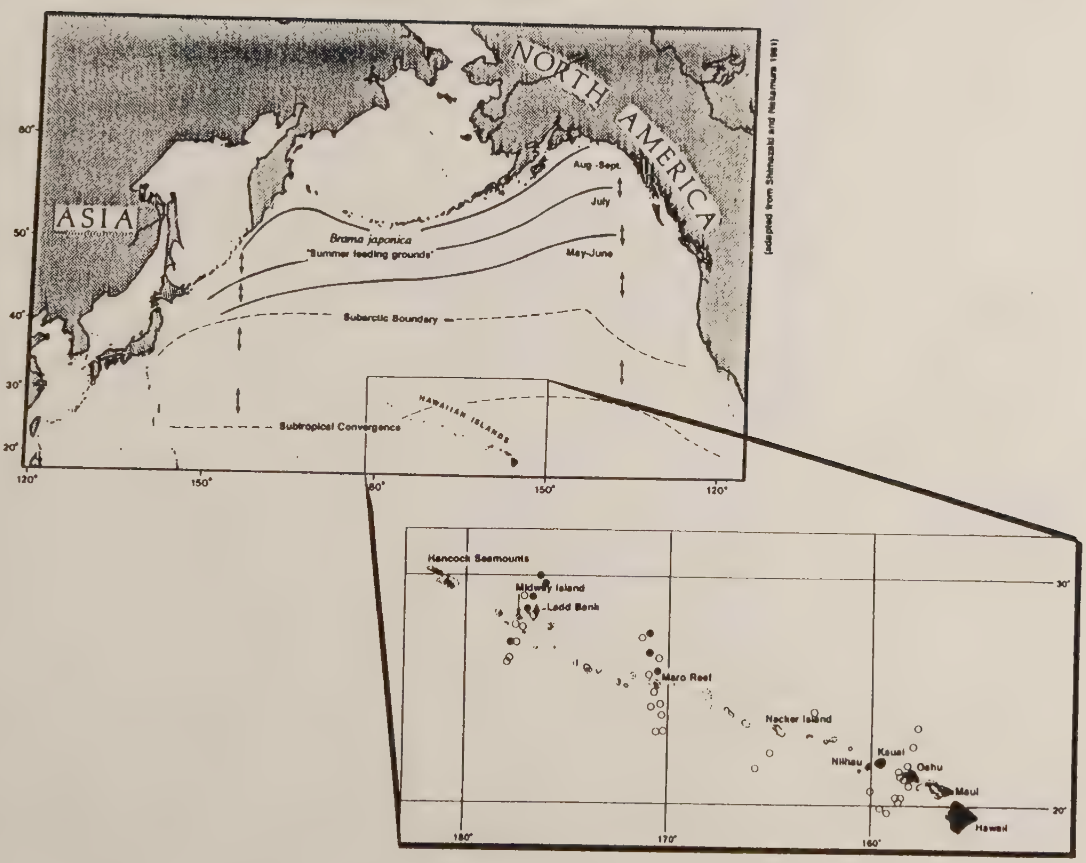
*Brama japonica*, like the flying squid *Ommastrephes bartrami* and other species of the North Pacific Transition Zone (NPTZ), migrate northward during summer months to feed along the Subarctic Frontal Zone (SAFZ). During the fall, *B. japonica* undergo a rapid southward migration towards the Subtropical Frontal Zone (STFZ), where spawning is hypothesized to occur during winter through early spring (Shimazaki and Nakamura 1981; Yoon and Shimazaki 1981) (Fig. 1).

Most knowledge pertaining to the life history and ecology of *B. japonica* has been based upon catch data and samples collected with driftnets during the summer feeding period near the Subarctic Boundary (Machidori and Nakamura 1971; Shimazaki and Nakamura 1981; Wada and Murata 1985; Shimazaki 1989). Limited information is available regarding the distribution, ecology, and life history of *B. japonica* during their winter and spring occupation of the STFZ. In this paper, we focus on the biology of *B. japonica* occupying the STFZ during winter. Preliminary results are presented on the ageing and distribution of the larvae and juveniles and the feeding ecology of the adults.

## III. MATERIALS AND METHODS

### 1. Larval and Juvenile Collection

During 25 February-21 March 1991, 40 tows with a modified pelagic Cobb trawl were conducted aboard the NOAA ship *Townsend Cromwell* in waters around the Hawaiian Archipelago (Fig. 1).


ASIA
NORTH AMERICA
60°
50°
40°
30°
20°
Aug.-Sept.
July
May-June
*Brama japonica*
"Summer feeding grounds"
Subarctic Boundary
Subtropical Convergence
HAWAIIAN ISLANDS
120°
150°
180°
150°
120°
Hancock Seamounts
Midway Island
Ladd Bank
Maro Reef
Necker Island
Niihau
Kauai
Oahu
Maui
Hawaii
30°
20°
180°
170°
160°

(adapted from Shimazaki and Nakamura 1981)

Fig. 1. *Brama japonica* seasonal distribution and collection locations of early life stages. Solid circles indicate positive midwater trawl tows, winter 1991; open circles indicate negative midwater tows; solid diamond indicates the capture location of two large (64.6 and 66.4 mm standard length) juveniles at Ladd Bank, April 1980.

The trawl is a basic dual warp midwater net, with a square mouth opening of approximately 140 m² when fishing (Wyllie Eche-verria *et al.* 1990; Lenarz *et al.* 1991) and is equipped with a cod-end liner constructed of 3.2 mm (1/8 in) knotless nylon delta mesh. During daylight hours, oblique tows targeted waters from the surface to 80 m depth, whereas at night, a horizontal tow in the upper 20 m was made by submerging the net just below the surface. All samples were frozen upon collection and returned to the laboratory for processing where late-stage larval and juvenile *B. japonica* were sorted and identified.

### 2. Satellite Oceanographic Observations

Satellite data were analyzed to characterize the mesoscale patterns of water masses and fronts in relation to the distribution of larval and juvenile *B. japonica*. Sea surface temperature (SST) measurements from NOAA-11 Advanced Very High Resolution Radiometer (AVHRR) images were obtained from satellite passes archived at the University of Hawaii's satellite oceanography laboratory. The SST measurements were integrated over 1.0 km², the area resolved by a single pixel on an AVHRR image; the accuracy of the SSTs measured by the NOAA-11 AVHRR was ±0.2°C.

### 3. Larval and Juvenile Age and Growth

Otoliths from early stages of *B. japonica* caught in Cobb trawls 204 km north of Maro Reef on 5 March 1991 (Fig. 1) were used for age determination. *Brama japonica* sorted from the trawl samples were fixed in 95% ethanol. Standard lengths (SL) of larvae from a broad size range were measured to the nearest 0.1 mm with an ocular micrometer and stereomicroscope. Both sagittal otoliths were extracted and mounted on microscope slides in clear resin (Eukitt). Thin sections in the sagittal plane were prepared following procedures outlined in Boehlert and Yoklavich (1985). Microstructural examinations were made with a compound microscope with polarized transmitted light at magnifications from 600-1500x (Fig. 2A). A conspicuous core area (Fig. 2B) was surrounded with a dark band. The radius of the core was 11-14 μm ($\bar{x}$ = 12.7 μm, $n = 25$) and was postulated to be a hatching mark. Growth increments were composed of alternating light and dark bands and were counted from the perimeter of the core to the otolith edge. Increments were counted by one observer at two separate reading sessions and averaged for a mean increment value. A linear model was fitted to the length-at-age data to describe larval and juvenile growth.

### 4. Feeding Ecology

Stomachs were examined from 76 adult *B. japonica* captured by large mesh (180 mm) surface gillnet aboard the research vessel *Shin-riasu maru*. Forty-four of the stomachs were extracted and frozen at sea from fish captured in the general vicinity of 30°N latitude and 170°E longitude on 18-22 January 1991. The remaining 32 were taken from fish captured and frozen whole at about 30°N latitude and 150°W longitude on 10-15 February 1991; stomachs were extracted in the laboratory. All of the *B. japonica* were sampled from driftnet sets deployed during 1500 and 1600 h and retrieved between 0000 and 0600 h. Samples were 39.0-48.3 cm fork length (FL) ($\bar{L}$ = 44.7, SD = 3.4).

Procedures for examining the stomachs were similar to those employed by Seki and Harrison (1989). Briefly, stomachs were first examined for the presence of food items; empty stomachs were noted and discarded. Food samples were sorted, counted, and identified to lowest practical taxon. Sorted prey items were blotted dry, and wet weights were measured to the nearest 0.1 g. Values of prey items were assessed by using percent of the index of relative importance (IRI) values, modified from Pinkas *et al.* (1971), which incorporates percentage by number (N), weight (W), and frequency of occurrence (F): IRI = %F(%N + %W).

## IV. RESULTS AND DISCUSSION

### 1. Larval and Juvenile Distribution

*Brama japonica* at early ontogenetic stages, including eggs, larvae, and juveniles, have been reported from single localities in the central North Pacific by Mead (1972); Loeb (1979a, b); and Seki and Mundy (1991). Our collections of larvae and juveniles are from a broad sampling range, providing insight into the vertical and spatial distribution of early life stages of *B. japonica* and consequently helping delineate spawning grounds and seasons of the species.

A total of 148 larval and juvenile *B. japonica* (Fig. 3A), from 9.8 to 34.0 mm SL ($\bar{L}$ = 14.2, SD = 3.2), were collected from 8 locations (Table 1). Although sampling was conducted north and south through much of the Hawaiian Archipelago, all but one of the *B. japonica* were collected from stations 28, 113, and 204 km north of the 183 m (100 fm) contour at Midway Islands and Maro Reef. The SSTs at these stations typically were 17.5°-19.8°C, with the mixed layer typically extending to about 100 m. No *B. japonica* were captured at any stations south of Maro Reef (ca. 25°30'N) where surface temperatures exceeded 21°C.

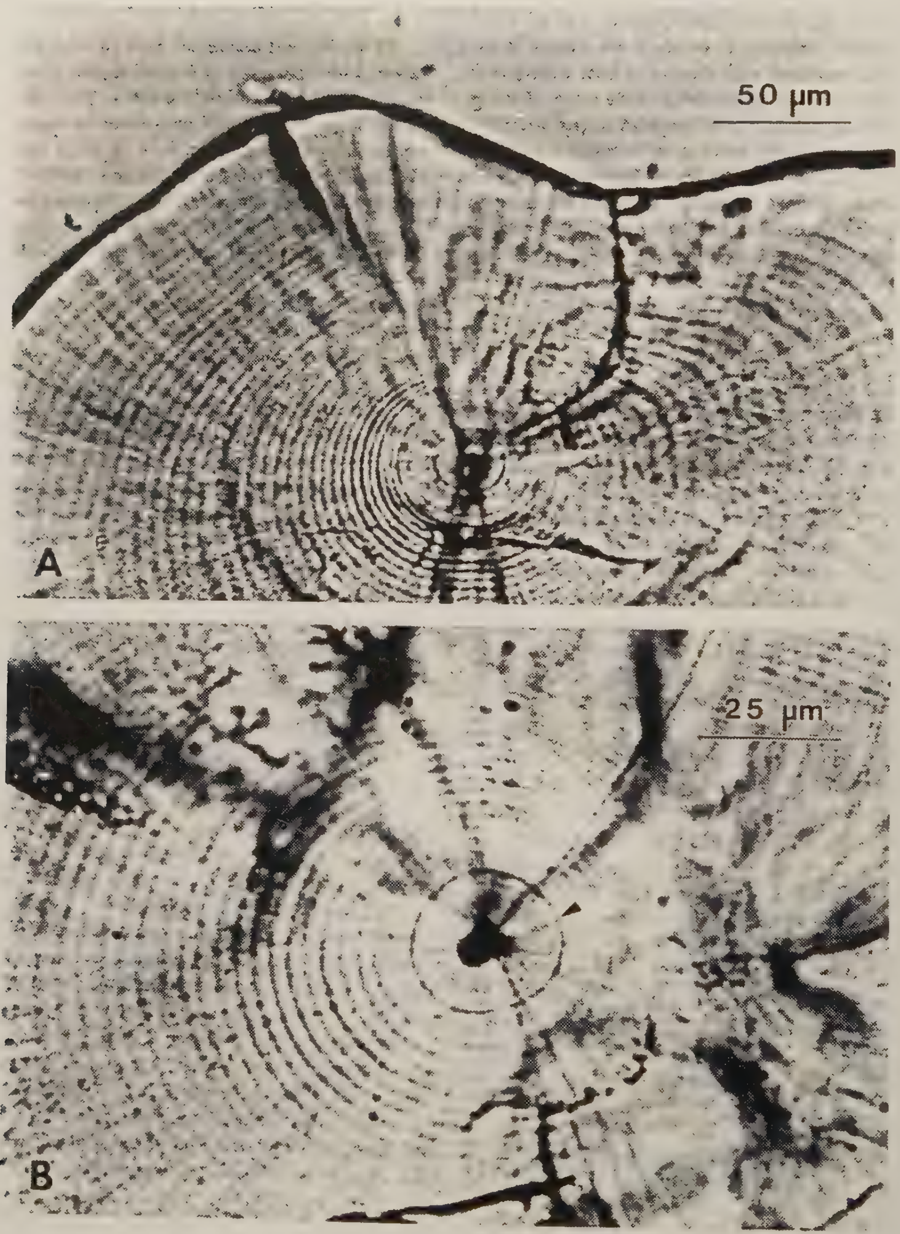


Fig. 2. Light micrographs of sagittal sections of otoliths from larval *Brama japonica*. (A) Growth increments from a 12.3 mm standard length larva. Duplicate increment counts were 40 and 41. (B) Central core area (arrow) was separated by a well-defined, dark band from the outer zone.

Table 1. Collection data from positive tows for large larvae and juvenile *Brama japonica* captured during March 1991 in the vicinity of the Hawaiian Archipelago (SL = standard length, SST = sea surface temperature, N = number of specimens).

| Day | Time(h) | Location (start)<br>Lat.(°N) | <br>Long.(°W) | N | SL(mm) | SST(°C) |
|---|---|---|---|---|---|---|
| 4 | 1721-1930 | 25°50.9' | 170°28.7' | 11 | 10.6-11.8 | 19.8 |
| 5 | 0805-1009 | 27°27.8' | 170°56.0' | 48 | 10.8-34.0 | 17.7 |
| 6 | 1716-1912 | 30°03.2' | 176°23.4' | 12 | 11.8-22.0 | 17.5 |
| 7 | 0820-1006 | 28°32.2' | 177°02.1' | 24 | 9.8-16.5 | 18.4 |
| 8 | 1500-1712 | 27°04.1' | 177°36.2' | 1 | 13.1 | 21.3 |
| 9 | 1002-1158 | 29°12.0' | 176°44.6' | 49 | 10.4-21.0 | 18.0 |
| 9 | 2010-2214 | 29°42.0' | 176°59.9' | 2 | 12.3-12.5 | 18.0 |
| 11 | 1049-1245 | 26°44.2' | 171°02.7' | 1 | 11.2 | 18.2 |

This corroborates the reported southern distributional limit of *B. japonica* at the 21°C isotherm (Mead 1972).

Because of cloud contamination, most AVHRR images corresponding to the *B. japonica* capture dates (4-11 March 1991, Table 1) were unusable; however, a satellite pass on 3 March 1991 at 1500 h provided good coverage of the area where *B. japonica* were captured (Fig. 4). The difference in color in Figure 4 indicates a change in SST; clearly evident is the Subtropical Front between 26° and 28°N. The distribution of larval and juvenile *B. japonica* revealed that nearly all captures occurred in cold (17°-18°C) water to the north of the Subtropical Front. The AVHRR image from 3 March was likely representative of the mesoscale SST distributions, since shipboard SST measurements at capture locations of *B. japonica* corresponded well with SSTs derived from the AVHRR image.

Nearly all of the *B. japonica* were taken in oblique tows conducted during daylight hours; two individuals at one location were taken within 20 m of the surface in a night tow. However, since early stages of *B. japonica* have been taken in both day and night oblique tows near Southeast Hancock Seamount (29°47'N, 179°03'E) (Seki and Mundy 1991), the near absence of *B. japonica* in the night tows was likely an artifact of the surface sampling (0-20 m) rather than differences due to diel presence or absence in the water column. Early stages of *B. japonica* reportedly are vertically distributed through most of the mixed layer, with no evidence of diel migration (Seki and Mundy 1991).

The size at which the juveniles begin migration north is not known. Two large juvenile *B. japonica* (64.6 and 66.4 mm SL; 77.3 and 78.4 mm FL; Fig. 3B) were collected in a fish trap within 95 m of the surface at Ladd Bank (28°30'N, 176°38'W; Fig. 1) on 24 April 1980. By comparison, Shimazaki *et al.* (1981) captured juvenile *B. japonica* as small as 160 mm FL in NPTZ waters near the Subarctic Boundary using nonselective surface gillnets (20 mesh sizes of 25-233 mm stretched mesh). Unfortunately, most knowledge of pomfret distribution and ecology in the NPTZ is based on fish captured with surface gillnets, and little information is available with regard to the vertical distribution of pomfrets below the 10 m fishing depth of the driftnets where smaller juveniles may occur.

## 2. Larval and Juvenile Age and Growth

Otoliths were examined from 32 *B. japonica* ranging from 10.8 to 24.1 mm SL. Mean increment counts ranged from 34.5 for the youngest larva to 62.0 for the oldest juvenile. Mean difference between increment counts was 2.16 increments. No validation experiment was conducted to determine the periodicity of increment deposition; increments were assumed to be deposited on a daily basis, because daily increment deposition within postlarvae of related species, *Coryphaena hippurus* and *C. equiselis*, have been validated in the laboratory (Uchiyama *et al.* 1986).

Estimated length-at-age data (Fig. 5) were described as follows:

$$SL_t = -1.77 + 0.353t ,$$

where $SL_t$ = standard length (mm) at age $t$. The coefficient of determination ($r^2$) was 0.70.

The growth model suggests that growth was 0.353 mm $d^{-1}$ for fish of 11-24 mm SL. Growth rates

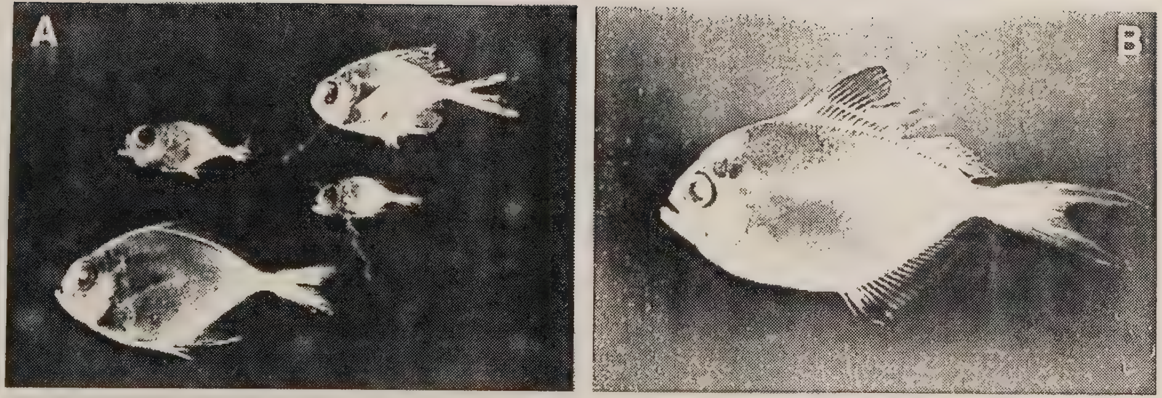


Fig. 3. Juvenile *Brama japonica*. (A) Juveniles of 15.1, 19.5, 26.0, and 38.6 mm standard length (SL) from prior collections at Southeast Hancock Seamount (29°47'N, 179°03'E; from Seki and Mundy 1991). (B) A 64.6 mm SL juvenile caught at Ladd Bank (28°30'N, 176°38'W).

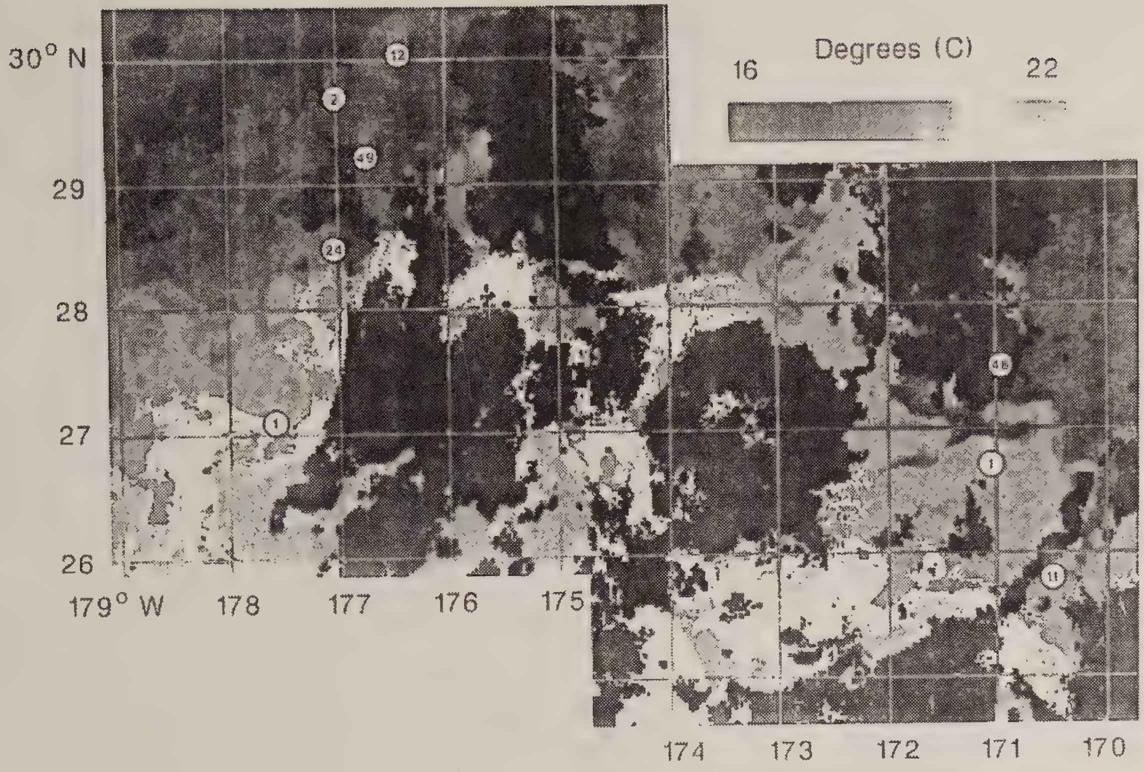

Degrees (C)
16
22
30° N
29
28
27
26
179° W
178
177
176
175
174
173
172
171
170
12
2
49
24
1
48
1
11

Fig. 4. NOAA 11 AVHRR image of sea surface temperature near the Northwestern Hawaiian Islands at 1500 h on 3 March 1991. Cold water is code in purple and blue and warm water in red; clouds appear black. Circles denote the locations where early stages of *Brama japonica* were captured; numbers indicate the number of individuals caught. (Satellite data provided by P. Flament, University of Hawaii, Department of Oceanography, Honolulu, HI 96822, U.S.A.)

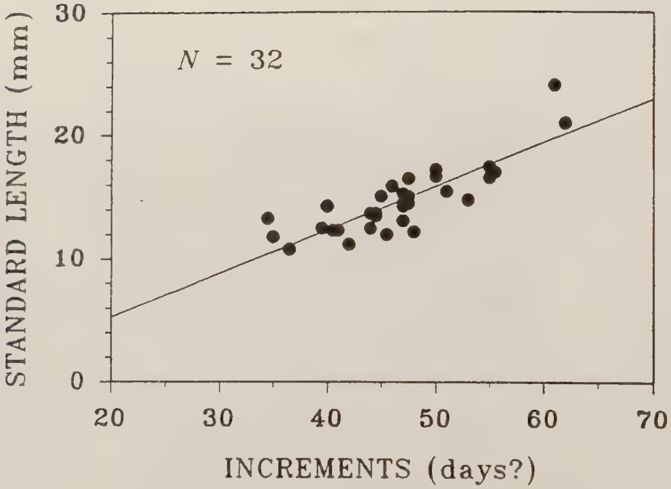


Fig. 5. Relationship between standard length and number of growth increments in otoliths from 32 larval and juvenile *Brama japonica*.

estimated using otolith microstructure from other perciform pelagic larvae and juveniles were 0.17 mm $d^{-1}$ for 1.6-19 mm *Leiostomus xanthurus* (Warlen and Chester 1985), 0.17 mm $d^{-1}$ for 2.5-6.0 mm *Trachurus symmetrics* (Hewitt *et al.* 1985), 0.33 mm $d^{-1}$ for 3-11.2 mm *Thunnus maccoyii* (Jenkins and Davis 1990), and 1.02-1.07 mm $d^{-1}$ for 12-48 mm *Coryphaena hippurus* and *C. equiselis* (Uchiyama *et al.* in prep.). While the comparison of growth in length is made difficult by the morphological diversity of larvae and the differences in environmental temperatures, the growth rate estimated for larval and juvenile *B. japonica* is within the range for related perciform species. The predicted fit of size at hatching was underestimated (-1.77 mm), as egg sizes in pomfrets range from 1.56 to 1.60 mm (Matarese *et al.* 1989) and larvae as small as 2.6 mm SL have been captured in the plankton (Seki and Mundy 1991). The size at hatching may have been underestimated either because of shrinkage of specimens in ethanol or the growth of early-stage larvae (preflexion) perhaps being slower than the modeled growth of larvae and juveniles.

Hatching date estimates, based on the ages of larvae and juveniles back calculated from the date of capture, ranged from 2 to 30 January 1991 when the first increment was assumed to be deposited at hatching. If the first increment was formed at a time after hatching (i.e., yolk-sac absorption, first feeding), then the actual hatching dates would precede the 2-30 January estimate. Hatching dates from our study correspond to those (November to May) of Shimazaki (1989), based on the back calculation of otolith increments from juveniles and adults and the period of reproduction (winter to early summer) predicted by Yoon and Shimazaki (1981).

## 3. Feeding Ecology

With regard to feeding ecology, only 14 (18.4%) of the 76 pomfret stomachs examined contained prey. No stomachs were replete from recent feeding, nor were any distended. Total weight of stomach contents ranged from 0.2 to 8.9 g ($\overline{W}$ = 3.5, SD = 3.1) and averaged 5.6 items (SD = 6.6). Unidentified crustaceans (%IRI = 47.8), hyperiid amphipods (%IRI = 19.3), and cephalopods (%IRI = 11.3) were the most important dietary components. Micronektonic fishes and pelagic tunicates represented the remainder of the identified stomach contents (Table 2). Debris items, such as plastic bag fragments and monofilament, also were found in the stomachs of three *B. japonica*, but were not considered prey (Table 2).

Little information is available on the feeding ecology of *B. japonica* during their southward winter migration. Qualitatively, Shimazaki and Nakamura (1981) reported that the diets of *B. japonica* caught in the subtropics during winter consisted of fish, squid, and other unidentified digested matter.

Table 2. Diet composition of 14 *Brama japonica* captured near the North Pacific Subtropical Frontal Zone, 18 January-16 February 1991 (IRI = index of relative importance).

| Prey species | N | %N | Weight (g) | % Weight | Frequency | %F | IRI | %IRI |
|---|---|---|---|---|---|---|---|---|
| Crustacea | 50 | 67.6 | 19.1 | 44.5 | 7 | 50.0 | 5605.0 | 47.8 |
| Hyperiidae | 33 | 44.6 | 7.3 | 17.0 | 4 | 28.6 | 1761.0 | 15.0 |
| Platyscelidae | 7 | 9.5 | 1.7 | 4.1 | 5 | 35.7 | 482.7 | 4.1 |
| Phronimidae | | | | | | | | |
| *Phronima sedentaria* | 1 | 1.4 | 1.1 | 2.5* | 1 | 7.1 | 27.5 | 0.2 |
| Sergestidae | 7 | 9.5 | 6.2 | 14.4 | 2 | 14.3 | 341.3 | 2.9 |
| Unidentified crustacean remains | 2 | 2.7 | 2.8 | 6.6 | 2 | 14.3 | 133.2 | 1.1 |
| Cephalopoda | 9 | 12.2 | 10.7 | 24.9 | 5 | 35.7 | 1324.5 | 11.3 |
| Onychoteuthidae | 4 | 5.4 | 7.1 | 16.6 | 1 | 7.1 | 157.2 | 1.3 |
| Histioteuthidae | 1 | 1.4 | 0.5 | 1.0 | 1 | 7.1 | 17.1 | 0.1 |
| Octopoda | 1 | 1.4 | 1.9 | 4.4 | 1 | 7.1 | 40.8 | 0.4 |
| Unidentified teuthoid | 3 | 4.1 | 1.2 | 2.8 | 3 | 21.4 | 147.8 | 1.3 |
| Pisces | 4 | 5.4 | 3.2 | 7.5 | 3 | 21.4 | 276.1 | 2.4 |
| Stomiiformes | 1 | 1.4 | 0.4 | 1.0 | 1 | 7.1 | 16.8 | 0.1 |
| Gempylidae | 1 | 1.4 | 2.2 | 5.2 | 1 | 7.1 | 46.4 | 0.4 |
| Unidentified fishes | 2 | 2.7 | 0.5 | 1.2 | 1 | 7.1 | 28.1 | 0.2 |
| Tunicata | 9 | 12.2 | 7.4 | 17.2 | 3 | 21.4 | 629.2 | 5.4 |
| Salpidae | 8 | 10.8 | 6.1 | 14.1 | 3 | 21.4 | 534.9 | 4.6 |
| Pyrosomatidae | 1 | 1.4 | 1.3 | 3.0 | 1 | 7.1 | 31.0 | 0.3 |
| Unidentified remains | 2 2.7 2.6 | 6.0 2 | 14.3 124.2 | 1.1 | | | | |
| Plastic | 3 | ---- | 5.0 | ---- | 3 | 21.4 | ---- | ---- |

*Includes "tunicate housing."

For *B. japonica* inhabiting the SAFZ waters during summer-fall, prior studies (Machidori and Nakamura 1971; Wada and Murata 1985; Kubodera and Shimazaki 1989; Shimazaki 1989) have reported that *B. japonica* feed on small pelagic fishes (sauries, sardines, myctophids, and juvenile mackerel) and small squids (gonatids and onychoteuthids). *Brama japonica* caught farther south during spring in the NPTZ feed on crustaceans and pteropods (Shimazaki and Nakamura 1981, Shimazaki 1989).

Shimazaki and Nakamura (1981) also reported high proportions of empty stomachs among *B. japonica* collected during winter (December-January) in the STFZ. The proportion of empty stomachs is comparatively much lower among *B. japonica* sampled near the Subarctic Boundary (Shimazaki and Nakamura 1981; Shimazaki 1989). Likewise, considerably fewer empty stomachs (46.2% were empty) have been found among pomfrets taken in the SAFZ during summer (Seki unpubl. data).

## V. ACKNOWLEDGMENTS

We gratefully acknowledge the help and kindness of many people, including the Fisheries Agency of Japan; officers and crew of the *Shin-riasu Maru*; officers, crew, and scientific field party of the NOAA ship *Townsend Cromwell* cruise 92-02; Pierre Flament and the University of Hawaii's Satellite Oceanography Laboratory; and Mr. Charles Holloway who sorted the samples.

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9384

# An Ecological Perspective on Inshore Fisheries in the Main Hawaiian Islands

M. KIMBERLY SMITH

*ABSTRACT—A description of fisheries within a depth of 100 fathoms is provided for the eight southeastern-most islands of the Hawaiian Archipelago, known as the main Hawaiian Islands (MHI). These are the inhabited islands of the State of Hawaii and are those most subject to inshore fishing pressure, because of their accessibility. Between 1980 and 1990, an average of 1,300 short tons of fishes and invertebrates were reported annually within 100 fm by commercial fishermen. Total landings may be significantly greater, since fishing is a popular pastime of residents and noncommercial landings are not reported. Although limited data are available on noncommercial fisheries, the majority of this review is based on reported commercial landings.*

*The principal ecological factors influencing fisheries in the MHI include coastal currents, the breadth and steepness of the coastal platform, and differences in windward and leeward climate. Expansive coastal development, increased erosion, and sedimentation are among negative human impacts on inshore reef ecosystems on most islands. Commercial fisheries for large pelagics (tunas and billfishes) are important in inshore areas around Ni'ihau, Ka'ula Rock, Kauai, and the Island of Hawaii (the Big Island), as are bottom "handline" fisheries for snappers and groupers around Kauai and Molokai. However, many more inshore fishermen target reef and estuarine species.*

*Two pelagic carangids, "akule,"* Selar crumenopthalmus, *and "opelu,"* Decapterus macarellus, *support the largest inshore fisheries in the MHI. During 1980-90, reported commercial landings within three miles of shore averaged 203 and 125 t for akule and opelu, respectively. Akule landings are distributed fairly evenly throughout the MHI, while more than 72% of the state's inshore opelu landings take place on the Big Island. Besides akule and opelu, other important commercial fisheries on all the MHI include those for surgeon, soldier, parrot, and goatfishes; snappers; octopus, and various trevallies. Trends in reported landings, trips, and catch per unit effort over the last decade are outlined for these fisheries. In heavily populated areas, fishing pressure appears to exceed the capacity of inshore resources to renew themselves. Management measures are beginning to focus on methods of limiting inshore fishing effort, while trying to maintain residents' access to fishing.*

## Introduction

### Regional Geography and Fishing Pressure

The volcanic peaks and platforms that make up the Hawaiian Islands rise from the ocean floor between roughly lat. 19–28° N and long. 155–178° W, giving the archipelago a length of close to 1,500 miles. However, almost all of Hawaii's population and land mass (above sea level) is concentrated on eight islands, located within 300 miles of the southeastern tip of the island chain (Fig. 1). These are the main Hawaiian Islands (MHI), which include Hawaii, Maui, Lanai, Kaho'olawe, Molokai, Oahu, Kauai and Ni'ihau. They are distinguished geologically and for management purposes from the submerged islands and atolls northwest of Kauai (beginning with Nihoa), known as the Northwestern Hawaiian Islands (NWHI).

Accessibility and rates of exploitation of Hawaiian inshore fisheries are determined largely by regional geography. Emergent portions of the NWHI are minimal, are exposed to treacherous northerly storms, and offer only limited freshwater and vegetation. These are some of the reasons the NWHI are largely uninhabited by humans. Travel from populated islands can take from days to weeks, depending on the size and condition of the vessel. Because of the distances involved, commercial fishermen with large vessels are essentially the only participants in NWHI fisheries.

The NWHI are an important breeding and resting ground for monk seals, green sea turtles, and various migratory seabirds whose natural habitat has been disturbed because of human activity in the MHI (Balazs, 1980; Gilmartin et al., 1980; Harrison and Hida, 1980). Most of the inshore area is part of the Hawaiian Islands National Wildlife Refuge (designated in 1909 by President Theodore Roosevelt as a bird refuge), managed by the U.S. Fish and Wildlife Service (USFWS). To maintain a less disturbed environment for threatened and endangered species, recreational and commercial activities (including fishing) are not allowed within the 10–20 fathom isobath of most islands northwest of Kauai (varying with location). Because of this, inshore fisheries in the NWHI are largely unexploited.

Inshore fish and invertebrate resources in the NWHI include many popular MHI species, such as a'ama crab, *Grapsus grapsus*; ahólehóle, *Kuhlia sandvicensis*; striped mullet, *Mugil cephalus*; and moi, *Polydactylus*

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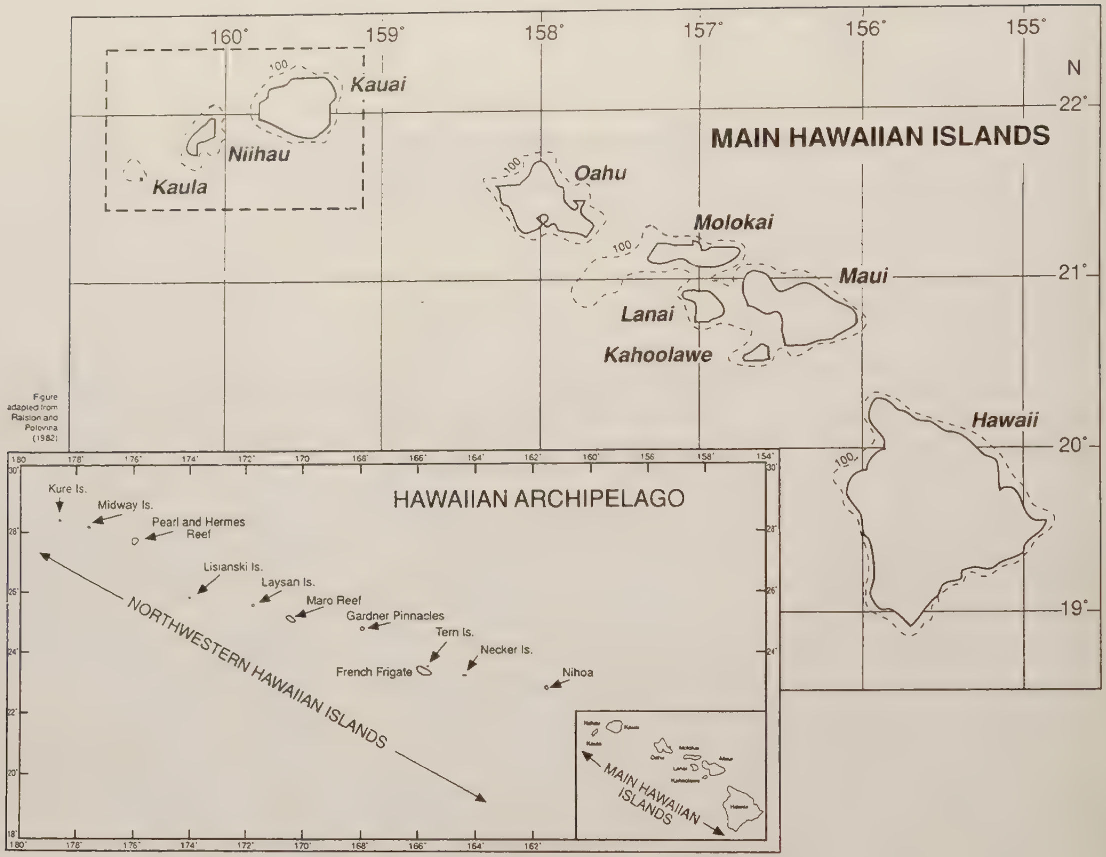
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Molokai
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Lanai
Kahoolawe
Hawaii
HAWAIIAN ARCHIPELAGO
Kure Is.
Midway Is.
Pearl and Hermes Reef
Lisianski Is.
Laysan Is.
Maro Reef
Gardner Pinnacles
Tern Is.
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Figure adapted from Ralston and Polovina (1982)

Figure 1.—Hawaiian Archipelago showing main Hawaiian islands.

*sexfilis* (Okamoto and Kanenaka, 1984). Spiny lobster, *Panulirus marginatus*, various eteline and lutjanid snappers, jacks, groupers, and large pelagic fishes are found slightly farther from shore (Uchida and Uchiyama, 1986), just as is seen in the MHI. These and other inshore fisheries in the MHI, where they are harvested, are the subject of this review.

## Climate, Coastal Topography, and Inshore Fishery Habitats

Inshore fisheries will be defined for this review as those within the 100–fm contour. This arbitrary boundary is found within three miles of shore throughout most of the MHI. Its correspondence with the offshore limit of state waters is convenient, although many inshore species migrate freely across the three-mile boundary. Normally the continental shelf is used as a guideline for the limit of inshore fisheries; however, these volcanic islands have no continental shelf. Gosline and Brock (1976) also selected the 100–fm isobath as an outer boundary, justifying this in part because it was the maximum depth fished by traps and handlines at that time. Modern hydraulic gurdies have extended the depth limit for fishing somewhat, but 100 fm is still a reasonable limit for small boat inshore fisheries (Squire and Smith, 1977).

Depth profiles, climate, and terrestrial influences are important determinants of the distribution of inshore fisheries in the MHI. The importance of coastal topography and hydrography may be accentuated by Hawaii's relative isolation in the northern tropical Pacific. The attraction of some pelagic species toward land formations (Murphy and Shomura, 1972) may also enhance inshore fishing opportunities.

The climatic pattern, which affects the distribution of terrestrial and aquatic communities throughout the MHI and most of the northern tropical Pacific is determined by prevailing trade winds. Wind-born weather fronts lose some of their moisture in passing over the mountainous portions of islands in this region. Thus, windward (northeastern) slopes have higher rainfall than leeward (southwest-facing) slopes. Because of this, windward embayments tend to support more estuarine fisheries than leeward areas.

Although high rainfall, erosion, and sedimentation are antagonistic to the survival of healthy corals, the coastal shelf also sustains fringing and patch reefs in windward regions. These habitats support rock- and crevice-dwelling organisms, such as octopus, crabs, and lobsters. The balance between the degree of protection from wind and waves, the amount of rainfall and sedimentation, and the availability of shallow shelf influences the extent of reef development in windward and leeward areas.

There are few stream-fed estuaries in Hawaii. The most important freshwater input to inshore areas may well be through groundwater (Carlquist, 1980). Wherever sources of freshwater meet the ocean (particularly in embayments), fish such as the Hawaiian anchovy or "nehu," *Encrasicholina purpurea*; round herring, *Etrumeus micropus*; and gold spot herring, *Herklotsichthys quadrimaculatus*; return seasonally to spawn (Williams and Clarke, 1983; Clarke, 1989). More commonly, Hawaiian fishes use estuaries as feeding and nursery areas, and may spawn offshore (Clarke, 1991). Fishes which feed in Hawaiian estuaries include mullet, *Mugil cephalus*; Hawaiian flagtail, *Kuhlia sandvicensis*; bigeye scad, *Selar crumenopthalmus*; and various species of snappers and trevally. Schools of adults and juveniles are targeted by fishermen as they enter and leave embayments.

Substrate, current, shelter, and food preferences of Hawaiian fishes are among other factors that separate species guilds and fisheries in relation to habitat (Gosline and Brock, 1976; Squire and Smith, 1977). Despite its narrow shelf, a wide variety of submerged habitats can be found around the MHI. The lagoons, bays, and beaches that surround these islands vary in composition from sand and mud to rock and coral. Sandy corridors, rocky slopes, and outcroppings are inhabited by large carangids, snappers, and groupers which are harvested with bottom "handlines" (Ralston and Polovina, 1982). Kona crabs, *Ranina ranina*, are also caught in these areas (Onizuka[1]). Schools of goatfishes, small carangids, and the introduced blueline snapper or ta'ape, *Lutjanus kasmira*, are common closer to shore in open and embayed habitats.

Hawaiian reefs support diverse and colorful communities of tropical fishes, invertebrates, and marine algae, which vary as a function of the depth, exposure, and three dimensional relief of their habitat (Fielding and Robinson, 1987; Oishi[2]). Reef fishes and invertebrates include lobsters, crabs, octopus, surgeonfishes, parrotfishes, and cryptic nocturnal species such as glasseyes (*Heteropriacanthus cruentatus* and other priacanthids), soldierfishes, *Myripristis* spp., and squirrelfishes, *Sargocentron* spp. Many of these are targeted by pole-and-line fishing, trapping, or spearing; nets are also employed along the reef flats and edges, yielding much larger catches per gear-unit.

### The Main Hawaiian Islands

The MHI, or "high islands" (islands above sea level), represent the younger portion of the Hawaiian Archipelago. Because they have emerged in relatively recent geologic time, these islands have less well-developed fringing reefs and have not subsided as far below sea level as the NWHI. The MHI form natural geographic groups, unified by shared channels and portions of interisland shelf (Fig. 1), which include: 1) Ni'ihau, Ka'ula Rock, and Kauai (the Kauai Complex), 2) Oahu, 3) Molokai, Maui, Lanai, and Kaho'olawe, (the Maui Complex), and 4) Hawaii (the Big Island). These island platform groups are meaningful for the discussion of inshore fisheries because of the dispersal characteristics of Hawaiian fishes (Jordan and Evermann, 1905; Gosline and Brock, 1976). Fishing activity, navigable sea conditions, and movements of fishermen are closely tied to shallow coastal waters and thus are based within shared portions of coastal shelf (Squire and Smith, 1977; PAC[3]). County designations throughout the state also reflect these associations. Kauai and Ni'ihau are in Kauai County; Oahu is in Honolulu County; Lanai, Molokai, Maui, and Kaho'olawe are in Maui County; and the Island of Hawaii makes up its own county.

### The Kauai Complex

Kauai, Ni'ihau, and Ka'ula Rock (a small peak southwest of Ni'ihau) are located at the northwestern corner of the MHI, separated from the other islands by the 72–mile-wide Kauai Channel between Kauai and Oahu. Kauai is dominated by a single mountainous mass, cut by steep slopes and ridges, which occupies most of its central and western sectors. Most of Kauai's coastline has lush vegetation, high rainfall (600–700 inches annually on some parts of the island), strong currents, and precipitous drop-offs to oceanic depths. The windward coasts are shaped by seasonal flooding and stream input, providing avenues along which endemic gobies enter and leave their oceanic larval phase (Radtke et al., 1988; Kinzie, 1990). Intensive spawning and migration events stimulate inshore fisheries. During the breeding season, Kauai's northeastern to southern shores are a popular area for recreational fishermen targeting the gobiid *Awaous stamineus* (known as 'o'opu nakea). Although reef fishes are seen all around the island, the southwestern coast shows a stronger oceanic influence and supports more reef and coastal pelagic fisheries, including those for bigeye and mackerel scads, goatfishes, surgeons, and squirrelfishes. Thrownetting and spearfishing are also prevalent on Kauai's leeward coast.

Ka'ula Rock and Ni'ihau, with steep nearshore slopes are drier than Kauai. All three islands provide habitat for snappers and groupers, captured by bottom hook-and-line fishing (referred to as "handlining," although hydraulic gurdies are used). Ni'ihau also supports a significant fishery for Kona crab

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[1] E. W. Onizuka. 1972. Management and development investigations of the Kona crab, *Ranina ranina* (Linnaeus): Final Report to Div. Aquatic Resources, Dep. Land and Natl. Resources, State of Hawaii, 28 p.

[2] F. Oishi. 1992. Hawaii's marine life conservation districts. Div. Aquatic Res., Dep. Land and Natl. Resources, State of Hawaii, 18 p.

[3] Pacific Analysis Corporation. 1984. Status of commerical fishing in the State of Hawaii. U.S. Army Eng. Div., Pac. Ocean Corps, Ft. Shafter. Prepared by PAC, 68 p.

(Onizuka[1]). Depths of 100 fm are reached within two miles of the shore of all three islands that make up the Kauai Complex, broadening to within 3–5 miles on the north shore of Kauai.

### Oahu

Seventy-two miles southeast of Kauai and twenty-six miles north of Molokai (across the Kaiwi Channel), Oahu is home to about 75% of the state's 1.3 million inhabitants (DBEDT, 1990). Having sustained the largest population for more than a century, it has experienced the highest levels of fishing pressure and other human impacts of all the Hawaiian Islands. The impacts of human development on fish populations along Oahu's heavily populated coast have been noted since the turn of the century (Jordan and Evermann, 1905). Artificial islands and airstrips have been built over reefs, bays, and sandbars on Oahu's leeward side; commercial and private piers, loading docks, high-rise hotels, and heavily populated beaches have overrun the natural shoreline. Dynamite was used to carve shipping channels into the reefs of Kaneohe Bay, on the windward coast, and the resulting coral rubble was placed into various landfills along its shoreline (Devaney et al., 1982). Coastal sites invaded by urban development include many ancient Hawaiian fishponds. In spite of congestion, residents can be found fishing from shore at all times of the day and night, especially along the less developed windward coast. Fishermen using light tackle line the windward shore during summer runs of oama and hahalalu (juvenile goatfish and bigeye scad).

The coastal shelf around Oahu is broader than that of the Kauai Complex, particularly at its prominent points. However, the 100–fm contour is still within three miles of shore in most areas. Bottom handlining, spearing, and trapping are among fisheries which depend on Oahu's relatively wide coastal shelf. Surround net and gill net fishing also take place on this shelf in embayments and along the edges of reefs.

Parallel mountain ranges, running northwest to southeast, determine Oahu's pattern of leeward and windward climate. Its northern and northeastern shores are strongly influenced by stream, surface, and groundwater input, seasonal storms, flooding, and high waves. Windward fisheries include several for estuarine species, such as mullet, crabs, carangids, octopus, sardines, and anchovies. The climate is generally drier on the southwestern side of the island, supporting more typically marine fisheries. However, Pearl Harbor in the middle of Oahu's leeward shore is the state's largest estuary.

Together, Pearl Harbor and Kaneohe Bay represent over 80% of true estuarine habitat in Hawaii. Kaneohe is a windward embayment containing a sandbar and many patch and fringing reefs. A unique mixture of corals and sediments, it has received decreasing amounts of fresh water and increased sediments over the years, owing to deforestation, erosion, and diversion of streams and groundwater to the leeward (more populated) side of the island. Despite decreased freshwater input, Kaneohe Bay is affected by seasonal floods which damage its coral reefs. Freshwater and sediment loading during floods has been intensified by channelization of streams and steeply graded urban development (Devaney et al., 1982; Gordon and Helfrich, 1970; OSP[4]). Freshwater input to Pearl Harbor has also decreased over the years. Together with marine pollution, this may have diminished its populations of estuarine fishes, such as mullet and certain carangids (Smith et al., 1973; Kimmerer and Durbin, 1975). Regardless of human impacts, both Pearl Harbor and Kaneohe Bay still support two of Oahu's largest and most diverse fisheries.

### The Maui Complex

On the southeast side of the Kaiwi Channel, Maui, Molokai, Lanai and Kaho'olawe form parts of a unified platform with a maximum depth of <100 fm. The Maui Complex has the widest coastal shelf of all the island platform groups. In some places (notably Penguin Bank), the 100–fm isobath is found over 30 miles from shore. The shallow, protected channels and beaches between islands provide a nesting and feeding ground for marine turtles, and a breeding and nursery ground for humpback whales. The channels and broad shelf are also a favorite fishing ground for full-time and experienced part-time fishermen, the latter known locally as the "weekend warriors."

Maui's dominant geological features are two volcanic peaks, Pu'u Ula'ula (Red Hill, on eastern Maui) and Pu'u Kukui (Candlenut Hill or the West Maui Mountains), united by a narrow land bridge. The double-mountain formation creates two natural embayments, windward Kahului and leeward Ma'alaea Bay. Maui's windward side is a lush, green agricultural area. Its leeward slopes are dry (but fertile) volcanic soil. Coastal soils have been heavily eroded by farming and development, as is common throughout the MHI. Spearfishing, surround and gill netting are the principal inshore methods used on the windward coast; while throw netting and handlining are popular on Maui's leeward shore. Due west of Ma'alaea Bay is Molokini Shoal, a unique and abundant area which is protected as a (State) Marine Life Conservation District (MLCD).

Molokai, the northernmost member of the Maui group, is also a double island. Its peaks, (western) Pu'u Nana and (eastern) Kamakou, are less than half the height of the mountains on Maui, giving the island a relatively dry climate and providing a less heterogeneous coastal habitat. Penguin Bank, on the western end of Molokai, is the most extensive shallow shelf area in the Hawaiian Islands. This bank supports a productive bottom "handline" fishery for snappers and groupers (Ralston and Polovina, 1982) and extensive net harvests of Kona crab (Onizuka[1]). Molokai is known for its numerous Hawaiian fishponds, many of which are now either partially or fully submerged. With fewer inhabitants and a closer adherence to traditional fishing methods than is seen on more populated islands, Molokai has fewer problems from overfishing of inshore habitats.

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[4] Office of State Planning. 1992. Kaneohe Bay master plan. Rep. of Kaneohe Bay Master Planning Task Force. OSP/Coastal Ocean, Reef and Island Advisors, Ltd., 171 p.

Kaho'olawe, now uninhabited, was taken over by the U.S. Navy in 1941 and used as a training area for more than 50 years (Clark, 1985). In 1968, the Navy began to reopen nearshore areas to fishermen and boaters. The island is gradually being reclaimed and debris (including monofilament line, plastic garbage, and unexploded ordnance), which accumulated during the military occupation, is being removed to eliminate the hazard to humans and marine life in the area.

Lanai, a small island west of Maui, is dedicated to agriculture. With the exception of the state harbor at Manele Bay, its entire coastline above the vegetation zone is private property. Access is mainly limited to resident workers and their guests. A few partially submerged Hawaiian fishponds are found on Lanai's eastern coast, where the fringing reef is farthest from shore. Quiet beaches on the western side of the island provide a nesting ground for green sea turtles. The southwestern shore supports another type of marine life refuge, the Manele-Hulopo'e MLCD.

### Hawaii, the "Big Island"

The Island of Hawaii, at the southeastern end of the Hawaiian Archipelago (across the Alenuihaha Channel), is known to residents as the "Big Island." Still volcanically active, the Big Island is dominated by two large dome volcanoes (Mauna Loa and Mauna Kea), and a few smaller ranges and craters. New beaches can be created in days or weeks on the southeastern coast, as a consequence of volcanic activity. The 100–fm isobath is found well within a mile of shore, from Kealakekua Bay on the western side and around the southern tip of the island to Cape Kumukahi. The coastal shelf widens to within 2–5 miles along the northern coast, from Cape Kumukahi to Kealakekua.

Wind and weather are particularly important along Hawaii's northeast shore, which receives year-round high rainfall, and periodic storm and seismic waves (or "tsunamis"). Windward Hilo Harbor supports extensive recreational and commercial fisheries for sardines, 'ama'ama (mullet), ahólehóle (Hawaiian flagtail), hahalalu (young bigeye scad), kuahonu crab, *Portunus sanguinolentus*; and Samoan crab, *Scylla serrata*[5]. Reef fishes are also caught on the open coast in this region.

The repercussions of land-based human activities in the Big Island's windward fisheries have been noted since the effluents of the sugar industry made streams and inshore areas uninhabitable to some fishes (Welsh[6]). These impacts have been mitigated to a certain extent over the years (Grigg, 1972, 1985), but have by no means been eliminated. Erosion and freshwater input via streams and groundwater influence nearshore ecology dramatically. The brown halo seen along the windward coast during rainy periods is an index of the magnitude of coastal erosion. Natural erosion has been intensified by the loss of forested areas to cattle ranching and agriculture. Additional environmental concerns for the Big Island's windward coast include those from toxics (DOH, 1981; Hallacher et al., 1985), sewage (Ambrose and Johnson, 1987), privately owned septic systems (Dudley et al., 1991), and petroleum derivatives from small and large vessels.

In contrast to the lush green valleys and raging rivers of the windward side, the Big Island's leeward (Kona) coast is flatter and drier and has more developed coral reefs. The inshore dropoff is particularly steep on the Kona Coast. Deep inshore waters and currents favorable to large pelagic fishes make it a preferred site for trollers and deep pelagic handline fishermen, who catch tunas, mahimahi, *Coryphaena hippurus*; and billfishes in this region. However, the most prominent inshore fisheries are those for smaller coastal pelagics, such as mackerel scad, *Decapterus macarellus*; and bigeye scad, *Selar crumenopthalmus*. Reef fish harvests of surgeon and soldierfishes are also significant in this area.

## Available Data

### Commercial Fisheries

Although anecdotal information is available, the only consistent long-term source of data on Hawaii's fisheries is the commercial landings database maintained by the State Division of Aquatic Resources (DAR, formerly the Division of Fish and Game). Anyone who catches and sells even one fish is considered a commercial fisherman and is required to report his or her landings and fishing effort on a monthly basis. The location of fishing activity is referenced to numbered geographic areas from the Commercial Fisheries Statistical Charts (DAR[7]), which are given to fishermen with catch report forms.

Despite legal reporting requirements, in practice there is considerable nonreporting. In the past, actual commercial landings may have been as much as double the amount reported for some species. Improved follow-up measures to track down licensed fishermen who fail to report have significantly increased the proportion of licensed commercial landings registered since 1989; however, other commercial fishermen remain unlicensed and commercial landings are still underestimated. Methods of improving the accuracy and completeness of commercial landings data are constantly under review (DAR[8]; Kasaoka[9]). Regional, seasonal, and short-term annual trends in these data are considered reliable and provide a plausible index of differences in commercial landings and fishing activity. However, recorded data would not represent total landings even if 100% reporting could be achieved, because there is no law to require recreational catches to be reported.

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[5] J. Kahiapo and M. K. Smith. In review. Recreational fishing survey of Hilo Bay: 1985–1990. Div. Aquatic Resources, 75 Aupuni St., Rm. 220, Hilo, Hawaii 96720, 41 p.

[6] J. P. Welsh. 1949. A preliminary report to the Division of Fish and Game Bait Program. Section 1. Summary of field work with special reference to Hilo Harbor nehu scarcity. Fish. Progr. Rep., Div. Fish Game, Bd. Comm. Agr. Forest, Hawaii 1(1), 25 p.

[7] Div. Aquatic Resources, State of Hawaii. 1990. Commercial fisheries statistical charts. Div. Aquatic Resources, Dep. Land and Natl. Resources, Charts A-H.

[8] Div. Aquatic Resources, State of Hawaii. 1984. Hawaii fisheries statistics design study. Div. Aquatic Res., Dep. Land and Natl. Resources, 187 p.

[9] L. D. Kasaoka. 1991. Revising the State of Hawaii's commercial fish catch reporting system. Final Report to Div. Aquatic Resources, Dep. Land and Natl. Resources, 466 p.

### Noncommercial (Recreational and Subsistence) Fishing

Hawaii is a state of fishermen and both recreational and "subsistence" landings are an important consideration. Actual "subsistence" fishing is rare. Most noncommercial fishermen fish either for enjoyment or to put food on the table, but do not rely on fishing as a source of food. Many are either retired or have a full-time job. Hawaii is one of the few U.S. coastal states which does not require a saltwater recreational fishing license. Because there are no recreational permitting or reporting requirements, it is difficult to estimate the number of recreational fishermen in Hawaii or their landings. Surveys indicate that 19–35% of residents fish (Hoffman and Yamauchi, 1972; USFWS, 1988). Estimates of recreational anglers alone were above 187,000 in the early 1980's (DAR[10]), as opposed to about 4,000 licensed commercial fishermen. Lal and Clark (1991) cited the State Department of Transportation and the U.S. Army Corps of Engineers as a source for an estimated 12,690 "personal boats," of which approximately 74% were engaged in fishing as their primary activity.

Recreational fishermen may outnumber commercial fishermen significantly, but per-trip landings are considerably lower. The difficulty in interpreting trends in total landings is compounded by differences in fishing gears and species targeted recreationally vs. commercially (SMS Research[11]; Samples and Schug[12]; Meyer Resources, Inc.[13]). Shoreline fishing with pole and line, trolling, spearfishing, throw netting, and crab netting are all popular activities of noncommercial fishermen. Surveys at Hilo, on the Big Island, show that 40–70% of shoreline fishing is conducted either with rod and reel or handpole (a bamboo pole without a reel) (Kahiapo and Smith, unpubl. data). This can be contrasted with an estimated 0.5% of commercial fishermen using light tackle in this area. Skillful fishermen, averaging 40–60 years of age, spend hours fishing patiently for 'ama'ama, hahalalu, crabs, and ahólehóle at Hilo and other areas throughout the state (Table 1 provides local and common fish names).

Differences in fishing areas, access methods, and target species of recreational fishermen mean their contribution to the total weight and species composition of landings must also be different. These differences make it impossible at present to interpret overall trends in landings and catch rates for species taken jointly by the recreational and commercial sectors. An independent estimate of recreational landings is needed. Only fragmentary information is presently available, but an effort is in progress to improve the data.

In the last 5–8 years, the DAR and the National Marine Fisheries Service (NMFS) have begun developing methods of estimating total landings through port and shoreline fishing (or "creel") surveys. Creel surveys involve field observation and interviews of recreational and commercial fishermen. Results of a pilot port-of-landing survey for greater Oahu show that some gears and species which are insignificant in commercial landings become important when total landings are considered (Hamm and Lum[14]). Inshore methods which are widely dispersed along the shoreline, such as spearing (for octopus and reef fishes), trapping (for small fishes), and handpicking (for marine algae) are particularly difficult to sample and may not show up at all in either commercial catch reports or port-of-landing surveys (Everson[15]). Shoreline creel surveys are now being conducted in several locations, including Kaneohe Bay (Everson[15]) and Waikiki (Yamamoto[16]; DLNR, 1992), Oahu; Hilo Bay, Hawaii (Kahiapo and Smith, unpublished data); and Hanalei and Nawiliwili Bays, Kauai. Fishery scientists may rely increasingly on information obtained through creel surveys to assist in interpreting reported data for estimates of overall landings for the state. Where data are available, recreational fisheries are included in the present discussion. However, it is important to keep in mind that the following summaries are based primarily on reported commercial landings.

### Sport Fishing

Besides residents, Hawaii supports an extensive gamefish charter boat industry catering to visitors. Samples et al.[17] estimated that 73,780 passenger-trips per year were completed during 1982, capturing about 2.2 million pounds of fish and $8.1 million in total revenue. It is common for the sport catch to become the property of the vessel and be sold by the captain. Charter boat operators are considered to be commercial fishermen (Hawaii Revised Statutes §189–2) and thus are required by law to submit catch reports

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[10] Div. Aquatic Resources, State of Hawaii. 1981. Management of Hawaii's coastal zone: Living marine resources. Div. Aquatic Resources, Dep. Land and Natl. Resources, 95 p.

[11] SMS Research. 1983. Experimental valuation of recreational fishing in Hawaii: Final Report. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Honolulu Lab., Southwest Fish. Sci. Cent. Admin. Rep. H-83–11C, 43 p.

[12] K. C. Samples and D. M. Schug. 1985. Charter fishing patrons in Hawaii: A study of their demographics, motivations, expenditures and fishing values. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent. Admin. Rep. H-85–8C, 95 p.

[13] Meyer Resources, Inc. 1987. A report on resident fishing in the Hawaiian Islands. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Honolulu Lab., Southwest Fish. Sci. Cent. Admin. Rep. H-87–8C, 74 p.

[14] D. C. Hamm and H. K. Lum. 1992. Preliminary results of the Hawaii small-boat fisheries survey. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Honolulu Lab., Southwest Fish. Sci. Cent. Admin. Rep. H-92–08, 35 p.

[15] A. Everson. 1991. Fishery data collection system for fishery utilization study of Kaneohe Bay: One year summary report. Hawaii Inst. Mar. Biol. NMFS job report to Div. Aquatic Res., Dep. Land and Natl. Res., 14 p.

[16] M. Yamamoto. 1990. Annual job progress report. Federal aid in sportfish restoration activities. Statewide Marine Research and Surveys Project F-16-R-15. Monitoring of Waikiki-Diamondhead FMA.

[17] K. C. Samples, J. N. Kusakabe, and J. T. Sproul. 1984. A description and economic appraisal of charter boat fishing in Hawaii. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Honolulu Lab., Southwest Fish. Sci. Cent. Admin. Rep. H-84–6C, 130 p.

Table 1.—Inshore commercial species by habitat, gear, and fishing method.

| Habitat | Fishing gear or method | Scientific name | Local name | Common name | Percent weight[1] |
|---|---|---|---|---|---|
| Shelf, slope and channel: Rocky to sandy bottoms | Bottom handline | *Etelis coruscans* | Onaga | Red snapper | 0.79 |
| | | *Etelis carbunculus* | Ehu | Red snapper | 0.23 |
| | | *Pristipomoides filamentosus* | Opakapaka | Pink snapper | 1.54 |
| | | *Pristipomoides sieboldii* | Kalekale | von Siebold's snapper | 0.14 |
| | | *Aprion virescens* | Uku[2] | Grey snapper | 1.33 |
| | | *Seriola rivoliana* | Kahala[2] | Amberjack | 0.53 |
| | | *Epinephelus quernus* | Hapu'upu'u | Seale's grouper | 0.13 |
| | | *Lutjanus kasmira* | Ta'ape[2] | Blue-line snapper | 2.80 |
| | | *Heterocarpus laevigatus* | Ono Shrimp | Deepwater shrimp | 1.39 |
| Coastal pelagic: Interisland channels and inshore areas right outside the reef | Surround net | *Selar crumenopthalmus* | Akule/Hahalalu[3] | Bigeye scad | 28.92 |
| | Purse seine | *Decapterus macarellus* | Opelu | Mackerel scad | 17.82 |
| | Pelagic handline | *Makaira mazara* | A'u | Blue marlin | 0.94 |
| | Trolling | *Tetrapturus audax* | A'u | Striped marlin | 0.17 |
| | Pole and line | *Xiphias gladius* | Shutome | Broadbill swordfish | 0.18 |
| | Palu'ahi (using fish chum) | *Thunnus albacares* | 'Ahi | Yellowfin tuna | 9.37 |
| | Ikashibi (using squid as bait) | *Thunnus alalunga* | Tombo | Albacore | 0.11 |
| | | *Katsuwonus pelamis* | Aku | Skipjack tuna | 1.65 |
| | | *Acanthocybium solandri* | Ono | Wahoo | 2.29 |
| | | *Coryphaena hippurus* | Mahimahi | Dolphinfish | 1.05 |
| | | *Euthynnus affinis* | Kawakawa | Bonito | 0.22 |
| | | *Sphyraena barracuda* | Kaku | Barracuda | 0.10 |
| | | *Sphyraena helleri* | Kawelea | Heller's barracuda | 0.27 |
| | | *Elagatis bipinnulatus* | Kamanu | Rainbow runner | 0.12 |
| Reef[6] and rocky: Open coast predominantly marine areas Juveniles in embayments | Handline | *Mulloides flavolineatus* | White/Green Weke | Yellowstripe goatfish | 2.39 |
| | Spear | *Mulloides pflugeri* | Weke-ula | Pfluger's goatfish | 0.71 |
| | Traps | *Parupeneus porphyreus* | Kumu | Whitesaddle goatfish | 0.57 |
| | Various nets | *Parupeneus multifasciatus* | Moano | Manybar goatfish | 0.39 |
| | | *Pseudupeneus cyclostomus* | Moano Kea | Blue goatfish | 0.15 |
| | | *Acanthurus dussumieri* | Palani | Eyestripe surgeonfish | 1.15 |
| | | *Acanthurus triostegus* | Manini | Convict tang | 0.60 |
| | | *Acanthurus xanthopterus* | Pualu | Yellowfinned surgeon | 0.30 |
| | | *Naso unicornis* | Kala | Unicornfish | 0.69 |
| | | | | Other surgeonfishes | 0.39 |
| | | *Myripristis berndti* & others | U'u (Menpachi) | Soldierfishes | 2.07 |
| | | *Scarus* spp.[4] | Uhu | Parrotfishes | 1.96 |
| | | *Atule mate* | Omaka | Yellow-tailed scad | 2.97 |
| | | *Caranx ignobilis* | White (Ulua/papio) | White trevally[5] | |
| | | *Caranx melampygus* | Omilu (Ulua/papio) | Bluefin trevally[5] | |
| | | *Caranx sexfasciatus* | Ulua Menpachi | Bigeye trevally[5] | |
| | | *Carangoides orthogrammus* | Papa (Ulua/papio) | Yellowspot trevally[5] | |
| | | *Gnathodon speciosus* | Pa'opa'o | Striped trevally[5] | |
| | | *Priacanthus meeki* and *Heteropriacanthus cruentatus* | Aweoweo | Red bigeye | 0.40 |
| | | *Bodianus bilunulatus* | A'awa | Blackspot wrasse | 0.17 |
| | | *Octopus cyanea* | He'e (Tako) | Octopus | 1.46 |
| Embayments[6] and estuaries: Including sand, mud, and patch reef habitats | Gill net | *Mugil cephalus* | 'Ama'ama | Striped mullet | 0.42 |
| | Surround net | *Polydactylus sexfilis* | Moi | Threadfin | 0.16 |
| | Paipai net | *Chanos chanos* | Awa | Milkfish | 0.09 |
| | Spearing | *Elops hawaiensis* | Awaawa | Ladyfish/Ten pounder | 0.05 |
| | Handpicked | *Kuhlia sandvicensis* | Ahólehóle | Hawaiian flagtail | 0.33 |
| | Handline | *Albula vulpes* | 'O'io | Bonefish | 0.58 |
| | Pole and line | *Ranina ranina* | Kona Crab | Spanner crab | 0.56 |
| | Casting and spinning | *Portunus sanguinolentus* | Kuahonu Crab | White crab | 0.29 |

[1] Percent weight = mean annual percent (by weight) of commercial landings reported between 1980–90 to the DAR in required Commercial Fish Catch Reports.

[2] Uku, kahala, and ta'ape come in quite close to shore as juveniles and adults.

[3] Adult and juvenile bigeye scad are referred to as "akule" and "hahalalu", respectively. Residents think of the two as distinct and report catches of each separately, as if they were different species.

[4] Parrotfishes captured are mainly *Scarus perspicillatus* and *Scarus sordidus*.

[5] The five species of trevallies listed make up more than 90% of "ulua/papio" landings. Omaka landings were also grouped as uluas since their juveniles may not always be distinguished in catch reports. Adult trevally and other jacks are referred to generally as "ulua"; juveniles as "papio". Kahala landings may also be placed into this group as juveniles because of their similar appearance, but they are separated in this table because of differences in adult habitat. It should be noted that the size at which fish become designated "ulua", rather than "papio" varies from island to island.

[6] There is some overlap in distribution between species listed under "reef" and "estuarine/embayment" habitats. Reefs and their fauna may also be found within embayments and estuaries in Hawaii.

(HRS §189–3). Thus, charter boat landings should be included in reported commercial data.

## Inshore Species

Table 1 summarizes local and common names of the principal inshore fishes as a function of depth and habitat. These 47 species represent 91% (by weight) of the state's inshore commercial landings. Individual reef species weigh a fraction of the average for coastal pelagics. Therefore, the weight of landings increases significantly in areas where large pelagic species are caught close to shore (such as on the Kona Coast). Landings in other areas represent a much larger number of organisms and many more hours of fishing effort. Unfortunately, available data do not allow an in-depth evaluation of mean size or numeric abundance, since fishermen often report only the number of pounds caught (most species are sold by weight).

Reef species make up a relatively small fraction of the total weight of landings, but market preferences increase the economic value of the reef catch. Goatfishes, such as kumu, *Parupeneus porphyreus*, and moano kali (or moano kea, *Parupeneus cyclostomus*), are targeted with traps and spears by inshore fishermen and sell for 2–6 times the price of other goatfishes, depending on the season. Prices for moano kali are the highest because these fish inhabit deeper water, making them more difficult to target.

Reported inshore landings by island platform groups (Table 2) illustrate the most important regional trends in weight and relative abundance of the top ten species in each area. Many species that are major constituents of inshore landings are also captured in significant numbers farther from shore. Because of their high mobility, the assessment and management of these stocks rely on collaboration between State and Federal agencies. Areas in the mid-MHI (Oahu and the Maui Complex), with more developed inshore shelf, fringing and patch reefs, sustain a larger proportion of landings of reef, shelf, and crevice-dwelling species, such as kumu, weke, u'u, ta'ape, palani, uhu, and he'e. The steep coastal slopes and swift currents of the Kauai Complex and the Big Island are a more suitable habitat for inshore pelagic species.

Akule, *Selar crumenopthalmus*; and opelu, *Decapterus macarellus*, landings rank within the top ten fisheries on all islands. From 1980 to 1990, reported commercial landings within three miles of shore averaged 203 and 125 tons for akule and opelu, respectively. Akule (bigeye scad) are the most productive inshore fishery throughout the MHI, except on the Big Island where more opelu (mackerel scad) are caught. Akule are captured with surround nets, made of either nylon or monofilament line (DLNR, 1992). Hoop nets are effective for catching opelu, which dive deeper when startled. Both species are also captured with hook and line. Night jigging with flies for akule and opelu on dark nights or during the new moon, using a small light to attract the fish (Kawamoto[18]), is extremely popular on all islands and among residents of all ages. Either a rod and reel or a simple bamboo "handpole" can be used.

Figures 2 and 3 show regional trends in landings of opelu and akule, respectively, from 1980 to 1990. More than 72% of the state's inshore opelu landings takes place on the Kailua-Kona Coast of the Big Island (Fig. 2). Therefore, trends in opelu landings are dominated by the success of the Big Island fishery. Akule landings (Fig. 3) are distributed fairly evenly throughout the MHI but are greatest on the Kailua-Kona Coast, at Ma'alaea Bay (on Maui) and Waianae (Oahu). Both fisheries have shown cyclical changes in abundance over the past 11 years, with peaks in 1983 and 1989. Changes in catch rates (CPUE, pounds/trip) are primarily responsible for the observed annual differences in catch, presumably because of actual changes in abundance of these highly mobile species in inshore areas. This trend is much stronger for the akule fishery. Regional trends in landings also vary somewhat from year to year (Fig. 2, 3). This is partly due to differences in seasonal migration patterns of the fishes around each island platform group and partly because of movements of a few large purse seiners.

**Table 2.—Mean annual landings (short tons) reported for 1980–90 by geographic region for Hawaii's principal inshore commercial species.**

| Island platform group | Principal Species[1] (descending order by weight of inshore landings) | | Mean annual tons[2] | Spp. freq.[3] (%) |
|---|---|---|---|---|
| | Local name | Scientific name | | |
| Kauai complex | Akule/hahalalu | *Selar crumenopthalmus* | 48.98 | 13.8 |
| | 'Ahi (yellowfin) | *Thunnus albacares* | 15.71 | 7.4 |
| | Opelu | *Decapterus macarellus* | 10.89 | 2.8 |
| | Ono shrimp | *Heterocarpus laevigatus* | 7.45 | 0.1 |
| | Ta'ape | *Lutjanus kasmira* | 5.69 | 3.5 |
| | White/green weke | *Mulloides flavolineatus* | 3.99 | 3.2 |
| | U'u | *Myripristis* spp. | 3.58 | 5.2 |
| | Ulua/papio | Primarily *Caranx* spp. | 3.55 | 7.8 |
| | Ono | *Acanthocybium solandri* | 3.18 | 4.2 |
| | Uku | *Aprion virescens* | 2.36 | 3.3 |
| Oahu | Akule/hahalalu | *Selar crumenopthalmus* | 67.40 | 11.9 |
| | Opelu | *Decapterus macarellus* | 18.97 | 6.8 |
| | White/green weke | *Mulloides flavolineatus* | 7.98 | 3.8 |
| | Ta'ape | *Lutjanus kasmira* | 6.77 | 4.0 |
| | He'e/tako | *Octopus cyanea* | 6.39 | 4.6 |
| | 'Ahi (yellowfin) | *Thunnus albacares* | 5.95 | 1.1 |
| | Palani | *Acanthurus dussumieri* | 5.29 | 3.3 |
| | Ulua/papio | *Caranx* spp. | 5.17 | 7.0 |
| | Aku | *Katsuwonus pelamis* | 4.78 | 0.5 |
| | Uhu | *Scarus* spp. | 3.85 | 2.4 |
| Maui complex | Akule/hahalalu | *Selar crumenopthalmus* | 52.36 | 4.2 |
| | Ulua/papio | *Caranx* spp. | 5.72 | 10.4 |
| | Shutome | *Xiphias gladius* | 5.01 | <0.1 |
| | Uhu | *Scarus* spp. | 4.74 | 3.5 |
| | Opakapaka | *Pristipomoides filamentosus* | 4.43 | 2.8 |
| | White/green weke | *Mulloides flavolineatus* | 4.07 | 3.7 |
| | Uku | *Aprion virescens* | 4.02 | 3.5 |
| | Opelu | *Decapterus macarellus* | 3.95 | 2.1 |
| | He'e | *Octopus cyanea* | 3.03 | 4.9 |
| | 'Ahi (yellowfin) | *Thunnus albacares* | 2.82 | 1.1 |
| Hawaii | Opelu | *Decapterus macarellus* | 91.18 | 14.4 |
| | 'Ahi (yellowfin) | *Thunnus albacares* | 41.42 | 5.7 |
| | Akule/hahalalu | *Selar crumenopthalmus* | 34.07 | 8.8 |
| | Ono shrimp | *Heterocarpus laevigatus* | 10.71 | 0.1 |
| | Ono (wahoo) | *Acanthocybium solandri* | 9.44 | 4.1 |
| | U'u | *Myripristis* spp. | 6.82 | 5.1 |
| | Ta'ape | *Lutjanus kasmira* | 5.61 | 5.0 |
| | Ulua/papio | *Caranx* spp. | 5.04 | 5.2 |
| | Opakapaka | *Pristipomoides filamentosus* | 4.29 | 3.9 |
| | Uhu | *Scarus* spp. | 4.07 | 2.0 |

[1] There are three multispecies categories (u'u, trevallies, and uhu). The species making up each of these categories are defined in Table 1.

[2] Mean annual tons = average annual weight of reported landings from 1980–90.

[3] Spp. freq. (%) = mean annual percentage of trips for 1980–90 which reported catching the species.

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[18] P. Y. Kawamoto. 1973. Management investigation of the akule, or bigeye scad, *Trachurops crumenopthalmus* (Bloch). Completion rep. for NMFS under Comm. Fish. Res. Devel. Act. P.L. 88–309. Proj. H-4-R, Div. Fish and Game, Dep. Land and Natl. Res., Hawaii, 28 p.

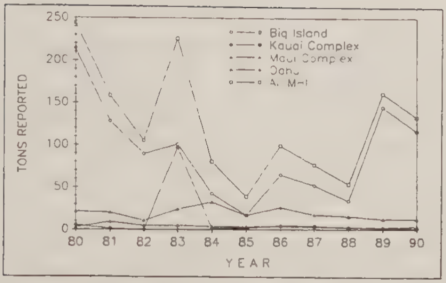

Figure 2.—Regional commercial landings of opelu in the main Hawaiian islands by island platform group.

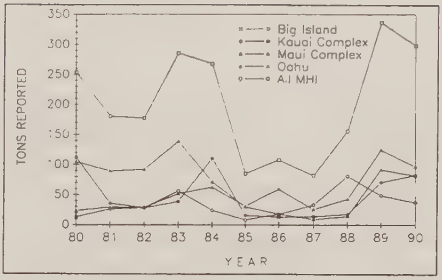

Figure 3.—Regional commercial landings of akule in the main Hawaiian islands by island platform group.

## Fishing Gears and Methods

Fishing gears employed in Hawaii include various pole-and-line methods (spin casting, handlining, or trolling) from shore, pier or platform, using motorized or unmotorized boats, canoes, kayaks, or surfboards. He'e (octopus), limu (algae), and cryptic fishes such as aweoweo (glasseyes) and u'u (soldierfishes) are speared or hand-collected by diving or swimming (with or without scuba). Trolling from windsurfers, canoes, and kayaks is used to capture ulua and papio near the reef drop-offs. Huge uluas, over 40 lb, are taken in this manner. Mahimahi, ono, and billfishes can be caught by moving slightly offshore, changing to lures or live bait, and by trolling with a high speed engine. The most extensive description of Hawaii's nearshore angling methods has been compiled by Rizzuto (1983, 1987, 1990). This information is complemented by Hosaka's (1973) publication and by popular televised programs that celebrate the art of Hawaiian fishing.

Table 3 summarizes the most common inshore commercial fishing gears by island platform group. Each group has unique fisheries characteristics, but there are more similarities than differences. The most important gear around all islands is the bottom handline. Trolling (for large pelagics) is the second most important fishing method on the Kauai Complex and the Big Island; diving, spearing, and other reef methods are second in importance around Oahu and Maui. Gill netting and related methods ranked third everywhere, except on the Big Island, where surround netting (for opelu) is more important. Throw netting is more prevalent around the Maui Complex than in other areas. There is not necessarily a direct relationship between gear frequencies and the proportion of landings by gear type. In fact, the least abundant gears often show the highest catch rates. Table 4 illustrates this, showing mean catch per unit effort (CPUE) and number of trips by gear type.

The relatively low proportion of trolling trips and high proportion of trapping around Oahu are both unique to this area. Oahu is also the only is-

Table 3.—Mean proportion of inshore commercial fishing trips by gear type and geographic region.

| | Relative gear abundance (% of annual trips[1]) | | | |
|---|---|---|---|---|
| Fishing gear/method | Kauai complex | Oahu | Maui complex | Hawaii |
| Aku boat (pole and line) | | 0.2 | <0.2 | <0.1 |
| Longline/flagline | | <0.1 | 0.2 | 0.1 |
| Drifting pelagic handline | 2.5 | 0.7 | 0.5 | 2.8 |
| Bottom handline | 42.4 | 46.2 | 33.3 | 56.1 |
| Kaka line/set line, ikashibi, palu'ahi | 0.7 | 0.3 | <0.1 | 1.3 |
| Trolling | 19.4 | 4.5 | 14.4 | 14.3 |
| Rod and reel (light tackle) | 0.1 | 0.2 | 0.2 | 0.5 |
| Trap | 1.9 | 10.7 | 3.0 | 0.8 |
| Diving (knife, spear, hand-picked) | 11.8 | 15.3 | 22.1 | 8.8 |
| Seine/gillnet/hukilau net | 12.5 | 12.1 | 14.9 | 2.7 |
| Akule/opelu/surround/purse nets | 2.1 | 2.7 | 3.5 | 8.8 |
| Throw net | 1.7 | 0.9 | 4.1 | 1.5 |
| Lobster/crab nets | 1.9 | 1.8 | 2.0 | 0.4 |
| Bait net | | <0.1 | | |
| Other and unspecified | 3.1 | 4.1 | 1.9 | 1.9 |

[1] Tabled values are the mean annual number of trips reporting each gear type from 1980 to 1990, expressed as a percentage of the total mean annual number of trips.

Table 4.—CPUE by gear type for principal fishing gears.

| | Annual mean (1980–90) | | |
|---|---|---|---|
| Geartype | Trips | Landings (lb.) | CPUE (lb/trip) |
| Aku boat (pole and line) | 36.3 | 10,245.6 | 282.2 |
| Longline/flagline | 30.3 | 8,648.2 | 285.4 |
| Drifting pelagic handline | 641.8 | 33,581.3 | 52.3 |
| Bottom handline | 8,976.8 | 426,581.4 | 47.5 |
| Kaka line/set line, ikashibi, palu'ahi | 87.2 | 15,992.3 | 183.4 |
| Trolling | 4,450.8 | 108,711.0 | 24.4 |
| Rod and reel (light tackle) | 114.5 | 1,141.4 | 10.0 |
| Trap | 371.1 | 57,078.4 | 153.8 |
| Diving (knife, spear, handpicked) | 1,154.4 | 91,660.6 | 79.4 |
| Seine/gillnet/hukilau net | 1,157.8 | 227,443.4 | 196.4 |
| Akule/opelu/surround/purse nets | 641.0 | 347,869.4 | 542.7 |
| Throw net | 681.5 | 7,843.4 | 11.5 |
| Bait net | 2.0 | 11.4 | 5.7 |
| Lobster/crab nets | 171.4 | 9,327.4 | 54.4 |

land supporting a major bait fishery at this time. Baitfishes (primarily nehu, or Hawaiian anchovy) were formerly harvested from Ma'alaea Bay, Maui (Nakamura, 1967) and other locations. These fisheries declined for marketing reasons during the mid-1980's (Kushima et al., 1992). Baitfishes harvested in Pearl Harbor and Kaneohe Bay are used to catch aku slightly offshore (Comitini, 1977), making Oahu the most important island for aku fishing. All aku boats presently have their home ports on Oahu.

Advances in the technology for fishing and locating fish are constantly increasing the efficiency of Hawaii's fishermen. Differences in the construction of fishing gears over the years have resulted in higher catch rates which, together with the rapidly increasing population, contribute to the potential for overfishing. For example, cotton or "linen" nets used by early Hawaiians have been replaced by monofilament nets which require less maintenance, bring in larger catches, and are less easily perceived by fish in clear water. Monofilament nets are employed along the reef faces, on the open coast and in embayments, both fixed (as a gill net) and to surround and bag fish schools (as a purse net) (DLNR, 1992). Paipai is another popular method of net fishing, whereby certain species (particularly weke) are herded into nets, either by divers or from a boat. The advent of monofilament line makes this method extremely effective, since the nets are essentially invisible in the water.

There are no trawl fisheries in Hawaii, since sharply sloping, coralline, or rocky coasts do not provide suitable substrate for trawl operations. Attempts at bottom and midwater trawling in the 1970's and 1980's were therefore abandoned. Bullpen nets are set in areas that are open and flat, facilitating the capture of large and highly mobile fishes. Sea turtles captured in bullpen nets, are easily released alive. Fish caught by surround methods can also be kept alive for long periods of time and released or harvested selectively. While many fish or turtles caught accidentally are released by conscientious fishermen, some die because people leave nets unattended or hold fish for long periods of time. This practice is particularly wasteful in Hawaii where the standard of quality for local fish consumption is high and where injured fish may not be marketable.

Other variations in fishing methods that influence catch composition include daytime vs. night fishing (and diving); diving with scuba; fishing with or without the moon; and carefully selecting seasons, tidal phases, and locations (Titcomb, 1952; Hosaka, 1973). All these tools are at the command of experienced fishermen in Hawaii, who pass on their special fishing secrets from one generation to another. Cultural heritage and family traditions, including preferences for certain species, are among the underlying factors that determine the composition of fisheries landings in Hawaii.

## Geographic Trends in Catch Rates and Fisheries Exploitation

Table 5 summarizes total reported landings and provides an index of commercial harvest rates within each island platform. The index, mean annual pounds per square nautical mile of shelf, was obtained by dividing reported landings by an estimated area for each coastal shelf, based on the difference between the area of land above sea level (DBEDT, 1990) and that of a circle enclosed by the 100–fm isobath. The length of the isobath for each platform group was taken from Ralston and Polovina (1982). Landings within three miles of shore were used for the Kauai Complex, Oahu, and Hawaii. For the Maui Complex, landings and estimated shelf area within 20 miles of shore were used owing to the extensive shallows of Penguin Bank.

The index indicates a higher rate of exploitation around Oahu, as would be expected because of its large population. Oahu's landings are accomplished

**Table 5.—Annual reported inshore and nearshore commercial landings and coastal harvest rates by geographic region.**

| Island platform group | Inshore landings[1, 2] (<3 n.mi.) | Nearshore landings[3] (3–20 n.mi.) | Total (0–20 n.mi.) | Length of 100 fm isobath[4] (n.mi.) | Estimated shelf area[5] (n.mi.$^2$) within 100 fm | Mean annual lb./n.mi.$^2$ of shelf[6] |
|---|---|---|---|---|---|---|
| Kauai complex | 260,313 lb.<br>18.56 % | 769,557 lb.<br>10.81 % | 1,029,870 lb.<br>12.08 % | 195 | 2,484 | 104.8 |
| Oahu | 372,042 lb.<br>26.53 % | 2,737,943 lb.<br>38.45 % | 3,109,985 lb.<br>36.49 % | 150 | 1,274 | 292.0 |
| Maui complex | 258,738 lb.<br>18.45 % | 1,197,168 lb.<br>16.81 % | 1,455,906 lb.<br>17.08 % | 390 | 11,080 | 131.4 |
| Hawaii | 511,506 lb.<br>36.47 % | 2,416,141 lb.<br>33.93 % | 2,927,647 lb.<br>34.35% | 290 | 3,187 | 160.5 |
| Total all island groups | 1,402,599 | 7,120,809 | 8,523,408 | 1,205 | 18,205 | 144.2[7] |

[1] Lb = mean annual pounds reported between 1980 and 1990 (all species).
[2] Inshore % = percent of total MHI landings reported within three nautical miles of shore.
[3] Nearshore % = percent of total MHI landings reported from 3–20 miles of shore.
[4] Length of 100-fm isobath = approximate nautical miles (from Ralston and Polvina, 1982).
[5] Estimated shelf area (ESA) = estimated square nautical miles of coastal shelf shallower than 100 fm.
[6] Mean annual lb./n.mi.$^2$ shelf = lb./ESA (landings within 20 n.mi. of the Maui complex included; only landings within 3 n.mi. for other areas).
[7] The all-islands total for "Mean annual lb/n.mi.$^2$" is based on a total of 2,599,767 lb. Landings greater than three miles from shore (nearshore) are not included for the Kaui complex, Oahu, and the Big Island.

by a large number of fishermen and catch rates per fishermen for comparable fishing effort are lower than on other islands. To compensate for this, Oahu's fishermen tend to use more fishing gear (considerably longer nets, more hooks, traps, etc.) and to fish for longer periods of time. Neighboring island residents are often astonished at the amount of effort invested by fishermen on Oahu. Reduced CPUE on Oahu may be an indication of adverse environmental impacts as well as overfishing. The Kauai and Maui groups show nearly equivalent annual landings within three miles of shore, but Maui's shallow depths extend to 3–20 miles from shore (and beyond). Once scaled to the total shallow shelf area, estimated annual catch rates (mean lb/n.mi.$^2$) around Maui are similar to those estimated for the Kauai Complex.

To evaluate catch rates around the islands, landings and CPUE (lb/trip) were summarized for the five most populated islands. Inshore catches and CPUE within 90° quadrants around each island are presented in Table 6. Trends for Kauai, Oahu, Maui, Molokai, and the Big Island indicate higher total landings and CPUE on the leeward (southwesterly) sides of all islands, in part because of increased landings of large pelagic species in this quadrant. However, there were also more trips recorded in most leeward areas. Increased pelagic productivity in leeward areas may be a function of localized upwelling and larval entrainment, driven by persistent (northeasterly) trade winds (McGary, 1955). Increased fishing activity in these areas probably results from improved sea conditions in the wind shadow of the islands, making leeward regions generally an easier place for small boats to troll and set nets. Other factors include accessibility from the shoreline and availability of launch ramps (PAC[3]). Because of their relative protection from winter storms, leeward areas are a more likely location for small boat harbors with associated launch facilities. The southwestern sector of most islands, which is also a somewhat sheltered quadrant, had the second highest number of trips.

Trends in inshore landings and CPUE from 1980 to 1990 were summarized for seven other important inshore species or groups (in addition to akule and opelu), which ranked in the top 10–20 consistently for three or more island platform groups. The groups selected were the white or green weke *Mulloides flavolineatus*; palani, *Acanthurus dussumieri*[19]; uhu, *Scarus* spp.; u'u, *Myripristis* spp.; he'e, *Octopus cyanea*; ta'ape, *Lutjanus kasmira*; and ulua/papio (jacks and trevallies, see Table 1). Statewide summaries only are provided here (Fig. 4 and 5), to show general trends in these fisheries. Regional mean CPUE by species groups are shown in Table 7. Catch rates were generally higher on Kauai and in the Maui Complex for all species.

Table 6.—Catch per unit effort (lb/trip) within 90° quadrants.

| Island Group<br>Quadrant | Mean annual lb. landed | Mean annual trips | Average CPUE (lb./trip) |
|---|---|---|---|
| Kaui | | | |
| I (Northeast quadrant) | 22,156 | 269 | 82.3 |
| II (Northwest quadrant) | 30,312 | 231 | 131.3 |
| III (Southwest quadrant) | 77,149 | 571 | 135.1 |
| IV (Southeast quadrant) | 33,854 | 336 | 100.8 |
| Oahu | | | |
| I (Northeast quadrant) | 59,568 | 539 | 110.5 |
| II (Northwest quadrant) | 51,866 | 500 | 103.6 |
| III (Southwest quadrant) | 107,933 | 1,442 | 74.8 |
| IV (Southeast quadrant) | 77,263 | 1,073 | 72.0 |
| Maui | | | |
| I (Northeast quadrant) | 17,167 | 219 | 78.2 |
| II (Northwest quadrant) | 64,223 | 491 | 130.3 |
| III (Southwest quadrant) | 106,188 | 399 | 266.3 |
| IV (Southeast quadrant) | 35,020 | 190 | 184.1 |
| Molokai | | | |
| I (Northeast quadrant) | 6,297 | 49 | 127.5 |
| II (Northwest quadrant) | 4,754 | 55 | 87.1 |
| III (Southwest quadrant) | 42,912 | 244 | 175.7 |
| IV (Southeast quadrant) | 8,256 | 125 | 66.1 |
| Hawaii (Big Island) | | | |
| I (Northeast quadrant) | 33,132 | 573 | 57.8 |
| II (Northwest quadrant) | 71,775 | 814 | 88.2 |
| III (Southwest quadrant) | 284,449 | 2,025 | 140.5 |
| IV (Southeast quadrant) | 77,878 | 965 | 80.7 |

Table 7.—Trends in catch per unit effort (lb./trip) from 1980 to 1990 for selected species by island-platform group.

| Species | Big Island | Kauai complex | Maui complex | Oahu | Mean All MHI |
|---|---|---|---|---|---|
| U'u | 36.39 | 52.5 | 27.87 | 13.07 | 29.95 |
| Ta'ape | 24.41 | 139.41 | 24.18 | 37.45 | 37.22 |
| Weke | 15.70 | 97.75 | 59.19 | 48.88 | 52.14 |
| Uhu | 42.04 | 32.90 | 63.66 | 27.34 | 40.03 |
| He'e | 13.71 | 26.95 | 28.42 | 26.94 | 26.74 |
| Palani | 20.38 | 39.05 | 20.53 | 35.15 | 29.37 |
| Ulua | 29.74 | 38.28 | 31.62 | 21.02 | 28.18 |
| Mean[1] | 26.05 | 61.04 | 36.50 | 29.98 | 38.39 |

[1] All species.

Reef fishes are most important on the islands of the Maui Complex and on Oahu. The highest volume of uhu were seen on all sides of Oahu, as well as at Kahului, Maui; and Kailua-Kona, Hawaii. Weke, palani, u'u, and uhu are abundant in both leeward and windward landings because of the presence of well-developed reef habitats in both types of areas. Most weke were caught on Oahu's northeastern and southeastern sides, on Kauai's eastern coast, and on western Maui. Landings of green weke (Fig. 4A) have shown a gradual decline since about 1983. This is primarily attributable to decreasing CPUE, because the number of trips has remained fairly stable. The number of trips has also remained constant for uhu (Fig. 4B), whereas reported landings have varied as a function of variation in CPUE. Palani landings (Fig. 4C) have shown a decline since 1986, but this has been due to decreased fishing effort (fewer trips), while CPUE has increased or remained the same.

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[19] It should be noted that two other surgeonfishes, known locally as "pualu" (*Acanthurus xanthopterus* and *A. mata*) are difficult to distinguish from the palani. Although separate records are kept when these species are reported separately, some pualu may be included in palani landings if they are not distinguished by fishermen.

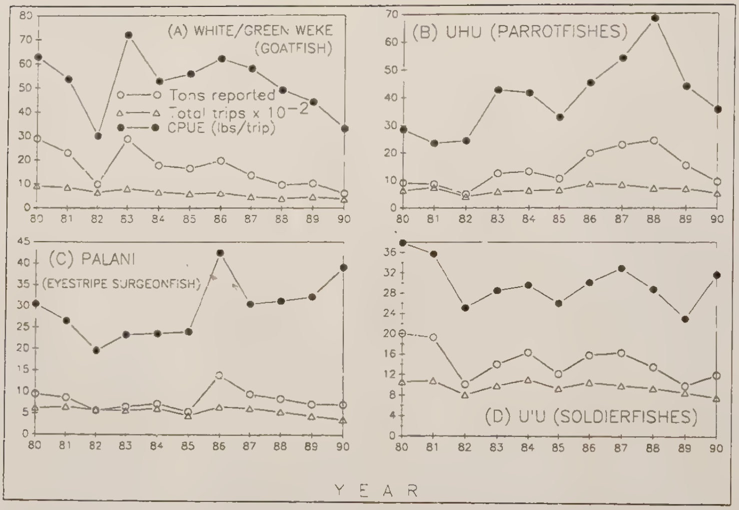

Figure 4.—Reported inshore commercial landings of selected species in the main Hawaiian islands.

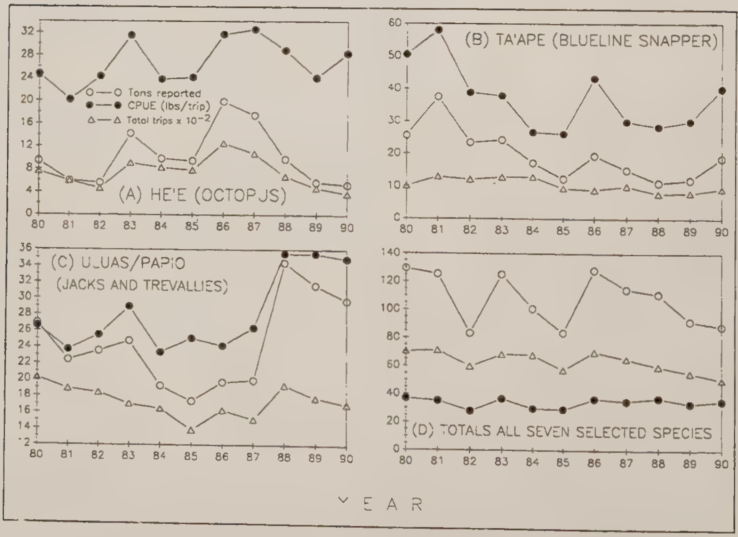

Figure 5.—Reported inshore commercial landings of selected species in the main Hawaiian islands.

The entire leeward coast of Oahu, windward and leeward Maui, and the Kailua-Kona Coast, have shown the highest landings of palani. U'u landings (Fig. 4D) have fluctuated over the years because of varying effort and CPUE.

He'e (octopus) is another reef species for which landings have fluctuated as a function of cyclical changes in the number of trips and the magnitude of CPUE. Figure 5A shows that the decline in reported landings since 1986 is due to fewer reported trips. However, this species is caught in large numbers by noncommercial fishermen (Everson[15]; Hamm and Lum[14]), and commercial trends do not tell the whole story. Kahului (Maui) registered the highest he'e landings in the state, followed by Kaneohe Bay (Oahu). Both are windward locations with a fairly wide shelf and reef area.

The introduced ta'ape are abundant everywhere, much to the dismay of residents who prefer native fishes (Kushima[20]). Reported landings (Fig. 5B) have been largely determined by fluctuations in CPUE. Ta'ape are caught in large numbers by surroundnet fishermen, who normally target akule. Their landings are limited primarily by the local market, which becomes flooded when too many fish are caught. Uluas were also important on all islands; however, noncommercial landings are an important component of this multi-species fishery. Ulua landings at Penguin Bank are roughly three times the volume recorded elsewhere, but the shelf area is also considerably larger. Figure 5C shows trends in ulua landings for all islands. The regional makeup of the catch by species indicates that the most diverse fisheries are found at Oahu and in the Maui Complex, followed by the Big Island, and finally Kauai. However, an in-depth evaluation of this group by species is limited by the tendency of fishermen to lump the fish together in their catch reports as simply "ulua" or "papio."

Total reported landings, trips, and CPUE for all seven species above are shown in Figure 5D, where an overall decline since 1986 is seen. While CPUE fluctuates or remains equivalent over the same period, the number of trips reported is steadily decreasing. The reason for this is unclear, but would seem not to indicate any cause for concern, since fishermen would appear to be voluntarily reducing their effort or merely switching to more lucrative offshore fisheries. However, it must be kept in mind at all times that reported commercial landings do not represent all inshore catch and effort. Another point worth noting is that the DAR began entering information on "no-catch" trips in the database in 1989. This information has not been included in the present summaries, but in the next decade its existence may allow a more accurate assessment of changes in CPUE.

## Additional Considerations

### Aquarium Landings

Although the foregoing summaries provide a brief insight into the makeup of Hawaii's nearshore commercial fisheries, there is much room for further consideration. No attempt was made here to summarize catches by aquarium collectors. Van Poollen and Obara (1984) profiled early economic characteristics of the marine aquarium industry in Hawaii. Aquarium landings are reported to the DAR and have been summarized by Miyasaka[21]. There were 231 aquarium collectors with permits in the State in 1988 (DLNR, 1988), of which 42% were commercial collectors. These fishermen reported catching 249,625 small fishes and invertebrates comprising about 215 species during 1988, of which 53% were collected from inshore areas on the Big Island's Kona Coast. The commercial value of these landings was estimated at $411,425 (all islands).

This is a rapidly expanding industry, responsible for an increasing proportion of the market value of commercial landings. A recent analysis provided by the DAR to the Kaneohe Bay Master Planning Task Force (OSP[4]) showed that while the total weight of commercial landings in Kaneohe Bay has declined over the last 12 years, aquarium collectors have increased the value of these landings, primarily through the sale of reef invertebrates. The desire to increase profits, however, cannot overshadow the need for resource conservation. Juvenile fishes are collected from inshore reefs, particularly along the leeward coast of the Big Island. Recent regulatory measures (DAR[22]) are aimed at moderating the impacts of these fisheries by controlling them in certain locations. Although the importance of aquarium fisheries cannot be overlooked, this topic merits a separate review.

### Markets

Local marketing opportunities for Hawaiian fishermen are limited, as might be expected in this isolated region. Each island has its own small markets, including spontaneous roadside ventures which spring up and disappear overnight. There are two principal auction houses, one on the island of Oahu and one on the Big Island. It is estimated that these two auctions are responsible for from 50 to 60% of fish sold commercially in the state. However, these markets cater to offshore fisheries and primarily service longline and bottom handline fishermen. Reef fishes are increasingly being sold directly to individual vendors.

A recent increase in the number of ciguatera poisoning incidents reported to the State Department of Health has resulted in alarm regarding the consumption of reef fish captured locally, dramatically reducing the marketability of some inshore species and shifting fishing effort to areas where there have been no reported incidents. Although the danger of ciguatera may be largely exaggerated, vendors prefer to err on the side of caution. Fish are also exported without passing through the local markets. The subject of markets and landings value will be treated in depth by another contributor to this volume and is also beyond the scope of the present review.

### Nonconsumptive Uses of Marine Fisheries Resources

Other important considerations in Hawaii include a variety of commercial nonconsumptive uses of inshore fisheries resources. Tourists enjoy activities designed to allow observation of reef fishes in their natural environment. This may be done from a boat or submersible, or by actually entering the water using a mask and snorkel. The lucrative industry associated with the latter type of viewing activity may involve bringing large groups of relatively inexperienced swimmers into contact with shallow inshore reefs, causing extensive trampling of fragile corals and destruction of the reef habitat. Both types of fish-viewing commercial tours generally involve some means of feeding the fish in order to concentrate them in an area where they can be seen. The result can be localized increases in abundance of the more aggressive and omnivorous species.

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[20] J. N. Kushima. 1989. Ta'ape market development project. Div. Aquatic Res., Dep. Land and Natl. Res., Hawaii, 29 p.

[21] A. Miyasaka. 1991. Hawaii's aquarium fish industry: A business profile. Div. Aquatic Res., Dep. Land and Natl. Res., Hawaii, 15 p.

[22] Div. Aquatic Resources, State of Hawaii. 1992. Regulations for the new Kona FMA. In press.

One of the present challenges to fisheries management in Hawaii is to preserve a healthy and abundant reef ecosystem that tourists can enjoy and at the same time allow fishing to take place at a reasonable level. The use of motorized recreational vehicles, such as jetskis and water skis, drives fish from the immediate area. Fishermen are responding to increased daytime commercial recreation by switching to nighttime fishing activity. Presumably fish viewing, ocean recreation, and fishing can coexist peacefully. Modern management measures must include setting allowable levels for ocean recreation, in addition to limits to fishing.

## Fisheries Management

### Status of Biological Knowledge of Stocks

Despite the importance and multiuse orientation of inshore resources, surprisingly little is known about the abundance and status of fisheries in Hawaii. Even generalized summaries of trends, such as are reported here, have rarely been attempted for inshore species. An exhaustive study would have to evaluate trends in these fish communities altogether, as an ecosystem. Changes introduced by humans in inshore habitat over the years may exert extremely important influences on fish abundance.

A DAR[10] report provided one of the most comprehensive summaries to date of the complex cultural, traditional, ecological, and jurisdictional issues involved in the management of Hawaii's inshore fisheries. In a survey fishermen described gear conflicts and reduced catches. Both fishermen and scientists expressed concern regarding whether the decline in nearshore fish populations might be due to increased fishing pressure and habitat alteration. The status of fishery resources was, and continues to be, viewed as a "barometer for the condition of our aquatic ecosystem." An examination of available (commercial) data at that time showed that fluctuating inshore fisheries landings were neither increasing nor declining significantly despite increased fishing effort. While CPUE was declining, it appeared that an equivalent amount of landings was being shared among an increasing number of fishermen. Various management scenarios were envisioned which would optimize CPUE for different sectors of the fishery and protect habitats critical to fish populations from the impacts of coastal development. The need for a careful evaluation of multi-species and multi-gear fisheries was stressed, as was the need for more complete and reliable fisheries data.

Shomura[23] summarized data from the State's commercial landings database, documenting an apparent decline in nearshore and both neritic and pelagic catches since the early 1900's. As in the DAR report, the data summarized by Shomura was in the form of statewide totals for many species and a wide range of geographic areas. Furthermore, no index of fishing effort was provided, making it difficult to interpret apparent trends. Shomura indicated that while deep slope and offshore pelagic landings had increased significantly, inshore and coastal landings were declining. The increase in offshore landings could be attributed to the effect of increased market demands on fishing effort. Decreasing reef fish landings might conversely be attributed in part to low relative demand for certain reef fishes, because of their distinctive flavor and odor of marine algae. Although local residents and native Hawaiians enjoy these distinctive tastes, tourists and foreign markets do not appreciate them.

The present summary, like those before it, encompasses a great deal of complexity which merits a more in-depth examination. As such, this review is considered to be a contribution to the understanding of trends in Hawaiian fisheries, indicating that assessment and management should be examined on a regional basis. While total landings for the state may have decreased since the early 1900's, regional evaluations show a wide range of variation. Some inshore fisheries show short-term improvements, although increased reporting may contribute to this apparent trend. The most disturbing trend is towards steadily increasing fishing effort in inshore ecosystems that are already heavily exploited. Most fisheries managers agree that fishing pressure should be reduced or limited in some areas in Hawaii; but answers to questions such as where, how much, and in what manner are still being sought.

### Ongoing Research

A project presently in progress, the Main Hawaiian Islands Marine Resources Investigation (MHI-MRI), is beginning to consolidate information on inshore fisheries and evaluate abundance, CPUE, and life history data for key species and areas. This project of the DAR is being conducted in collaboration with other fisheries management and marine research agencies statewide. Participants include the University of Hawaii Sea Grant College Program, Marine Option Program, Hawaii Institute of Marine Biology, and Hawaii Institute of Geophysics; the NMFS Southwest Fisheries Science Center, Honolulu Lab; the Oceanic Institute; the Western Pacific Regional Fisheries Management Council; and the USFWS Hawaii Cooperative Fisheries Research Unit. The project also cooperates with the International Center for Living Aquatic Resources Management (ICLARM) in the context of FISHBASE, a worldwide computerized database of biological information on fishes (Pauly and Froese, 1991), to obtain jointly a complete coverage of the fishes of the Central Pacific.

MHI-MRI will reevaluate the management of inshore fisheries throughout the MHI, and produce long-term recommendations to improve resource abundance and ensure sustainable fisheries. Research in progress seeks to define the principal causes of the declining abundance of some inshore species and to identify mitigative measures to offset negative impacts as needed. Overfishing, increased erosion and sedimentation, and both alterations and pollution of inshore habitats are among factors under investigation. Early indications are that limitation of fishing pressure, localized stock enhancement, and protection of inshore nursery areas from further human impacts could all contribute to recovery of inshore fish populations in Hawaii.

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### Regulatory Measures

Existing regulatory measures for Hawaiian inshore fisheries include bag limits, seasonal closures, and minimum size restrictions for capture and sale. Gear restrictions inside harbors allow pole-and-line fishing using only one pole with two hooks per fisherman. Crab netting in these areas must be limited to ten (small circular) nets per fisherman. Fishing regulations are summarized for the public in a brochure, updated annually by the DAR (DAR[24]). In addition to these regulations, there are specific gear restrictions in areas designated as Fishery Management Areas (FMA's) and MLCD's.

FMA's are established in areas where fishing or resource use competition is a problem and generally involve restriction of fishing gears or uses. Examples include the Waikiki-Diamond Head Shoreline FMA (Oahu) and Hilo Harbor FMA (Hawaii), where net fishing is restricted. The Waikiki-Diamond Head FMA rules rotate gear restrictions annually. Pole-and-line, thrownet or handnet fishing, and daytime spearing are allowed during even numbered years. No fishing is allowed in odd numbered years. Hilo Harbor FMA is regulated differently, tailored to the needs of local fishermen. In addition to bag limits, no gill, surround, or cross netting is allowed at any time within the Hilo breakwall, but all types of fishing are permitted year-round outside this area. Measures that regulate fishing pressure, while maintaining fishing opportunities for a variety of users, are more widely accepted in local communities. The benefits of these measures are demonstrated by an almost immediate increase in resource abundance, as indicated by increases in estimated biomass, in average and maximum size of fish captured, and in CPUE (Yamamoto[16]; Kahiapo and Smith[5]).

Molokini Crater, southwest of Maui, is a State-regulated MLCD. Only trolling is presently allowed in this partially submerged crater, which is a popular tour site for divers; but measures are being considered to restrict trolling as well. Other MLCD's and FMA's dot the coasts of the MHI (DAR[25]; Oishi[2]). Regulations are site specific, but generally, where fishing is allowed, it is restricted to pole-and-line, hand methods, and throw netting.

As seen under fishing methods, gears such as longlines, gill nets and surround nets are responsible for a large volume of landings in relation to the number of trips and fishermen. This is fine as long as the resource is not over harvested. These fleets are small and in some cases, such as for longline fishing, limited entry schemes are being developed to conserve resources for future generations. Other fisheries, such as surround netting, are presently limited by social constraints worked out through "gentlemen's agreements" between fishermen. As fishing pressure increases because of immigration and population growth, the need to formalize these agreements becomes increasingly important.

Ancient Hawaiians practiced seasonal closure of certain areas to fishing. Traditional systems provided for seasonal, species, and area-specific harvesting. The practices of sharing the catch, leaving certain species to royalty, and never taking more than was needed contributed to the balance between fishing and conservation in early times (Titcomb, 1952; Johannes, 1978). The loss of the traditional Hawaiian fishery management system and the failure to replace it with something comparable when Hawaii became part of the United States (Jordan and Evermann, 1905; Titcomb, 1952; Johannes, 1978; DAR[10]; Smith and Pai, 1992) are impacts from which nearshore living resources may take a long time to recover. A "kapuku" plan proposed in the late 1970's (HMR[26]) was one of the first attempts to restore a system of rotating area closures; however, agreement could not be reached on the specific areas to be closed. Present regulations, with rotating FMA's and MLCD's parallel this type of system on a small scale, but it is apparent that more protection of inshore resources is needed.

Because the jurisdiction of fisheries regulatory agencies in Hawaii is determined by geographic boundaries which do not coincide with the boundaries of migratory organisms that make up its fisheries, collaboration and cooperation between these agencies is critical to successful management. Environmental protection is another increasing concern that has demonstrated value to the conservation of inshore fisheries resources. Collaboration is being developed, and economic, scientific, and enforcement resources pooled, in order to manage the resources more effectively. It is clear from the long hours dedicated by the public to meetings designed to guide management efforts that residents are concerned about maintaining their rich and diverse natural heritage. The improved management of inshore fisheries and fishery habitats is an issue which must be resolved before the end of the present decade, and Hawaii's residents and resource managers are rising to meet the challenge.

### Acknowledgments

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# BALANCING SAMPLING PRECISION AND FISHERIES MANAGEMENT OBJECTIVES: MINIMAL METHODS

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## ABSTRACT

Density-dependent and environmental effects on population size are both too weak to be useful for short term fishery management (Smith, 1985). Year-to-year variation of recruitment rate may be of the same order of magnitude as measurement uncertainty and population changes may have to be sustained for 2 to 3 years to be detectable using the precision available from current techniques. As fishing rates accelerate, the dependence of the fishable biomass on recruitment is increased. Pre-recruit survival and growth may be more episodic than adult survival and fecundity (Smith and Moser, 1988). The episodic nature of recruitment combined with higher fishing rates may make more frequent biomass estimates necessary. When variable recruitment and high total instantaneous mortality rates (ITMR) reach a certain level, effective fisheries management will require development of recruitment prediction procedures in addition to virtual population and biomass monitoring. Annual biomass surveys may be redundant because many stocks contain several year classes. The costs of implementing recruitment prediction and systems to monitor biomass may be a significant fraction of the value of the added catch and this should be considered during management planning.

For many modern fisheries, overfishing occurs before effective management measures can be taken (Murphy, 1977). Traditional measures of overfishing, like declining size composition of the catch or declining catch per unit of effort of young fish, may not be sufficiently timely for fisheries on populations with short life cycles or in unstable habitats (Mangel, 1991). In the relatively short history of clupeoid fisheries there have already been many population changes of several orders of magnitude (Murphy, 1977; Lluch-Belda et al., 1989). One of the principal dangers of overfishing on these stocks is that the population distribution contracts into a small area where catch per unit of effort remains high even though the stock has declined to a small fraction of its original size (MacCall, 1990). Based on several decades of fisheries management experience on several stocks in the North Atlantic, it seems clear that neither density-dependent nor density-independent effects on population size will be sufficiently clear for predictive purposes of management (Smith, 1985).

It is the purpose of this paper to show how 1) the precision of biomass estimates, 2) the scale of short term changes in abundance and 3) mortality rates experienced by exploited stocks affect fisheries management.

## Accuracy and Precision

A typical response of a population to fishing mortality is a decrease in the relative contribution of the older fish to reproduction (Murphy, 1968). Under these conditions population estimates may need to be made more often. Decisions on the required frequency of biomass estimates could be based on the life history of the species under management (Garrod and Knight, 1979; Shelton, 1987; Smith and Moser, 1988) or on the time scales of variability in the environment (Bernal, 1981; Bernal and McGowan, 1981; Chelton et al., 1982; McGowan, 1989). In extreme cases, such as the fishery on Peruvian anchoveta (Pauly et al., 1987) the instantaneous total mortality rates (ITMR), fishing and natural, exceed a value of 1 and thus would appear to require more frequent spawning biomass estimates and recruitment prediction procedures to be managed successfully.

Table 1. Recruits as a fraction of the fishable stock under a wide range of annual instantaneous total mortality rates (ITMR)

| ITMR (Z) | Recruits as fraction of stock $(1 - e^{Z})$ | Years to 1% of recruited cohort size |
|---|---|---|
| 0.01 | 0.010 | 529 |
| 0.02 | 0.020 | 264 |
| 0.05 | 0.049 | 105 |
| 0.1 | 0.095 | 52 |
| 0.2 | 0.181 | 26 |
| 0.5 | 0.393 | 10 |
| 1 | 0.632 | 5 |
| 2 | 0.865 | 2 |
| 5 | 0.993 | 1 |
| 10 | 1.000 | 0 |

Population estimates from accurate methods such as virtual population analysis are often delayed for years and estimates from fishery independent methods like spawning biomass estimation or acoustic-trawl procedures may be overly expensive. Based on the best methods available (Bindman, 1986; Prager and MacCall, 1988; Hightower, 1990), it does not seem likely that coefficients of variation (standard error of estimate divided by estimate) less than 30% will be affordable by any method. This means that a fish stock could actually decline at a high rate but that conventional methods like virtual population analysis could not detect the decline for several years. Even direct spawning biomass estimates (Lasker, 1985), which provide an instantaneous estimate of spawning stock size in a given year, may not detect meaningful changes of population size for 1 or 2 years, given the limits of precision for a given cost. In addition to the "recruitment" problem on the short term, there will likely be a need to detect the onset of long term "climatic regime" shifts in fish production (Lluch-Belda et al., 1989).

## Natural and Fishing Mortality

When the fishery depends heavily on recruitment, management measures must be timely to respond to the usual recruitment variability (Hennemuth et al., 1980). For example, one could assume an exponential rate of decline of the cohort following recruitment at any age:

$$N_{t-t_0} = N_0 \cdot e^{-(F+M)\cdot(t-t_0)}$$

where $N_{t-t_0}$ is the number of fish remaining at time "t"; $N_0$ is the number of fish recruited; and, M and F are the instantaneous natural and fishing mortality rates. Thus, one can use the number of useful cohorts in a population (>0.5% of recruits remaining) under various conditions of M and F. Using the simplifying assumptions of 1) changes in total mortality are principally caused by changes in the rate of fishing, 2) the mortality is even with age following recruitment, and, 3) the number of recruits is the same at each time zero. Changes in the number of useful cohorts in the population result from any change of natural and fishing mortality rates: thus, an increase in either natural or fishing mortality rates will increase the dependence of the fishery on the newly recruited fraction of the stock.

Hennemuth et al. (1980) reported that recruitment per unit spawning biomass is log-normally distributed. This means that if the policy were adjusted to reflect the spawning biomass estimated in the preceding year plus an allowance for an "average" recruitment, one should anticipate an occasional high recruitment but a majority of recruitments would be well below "average."

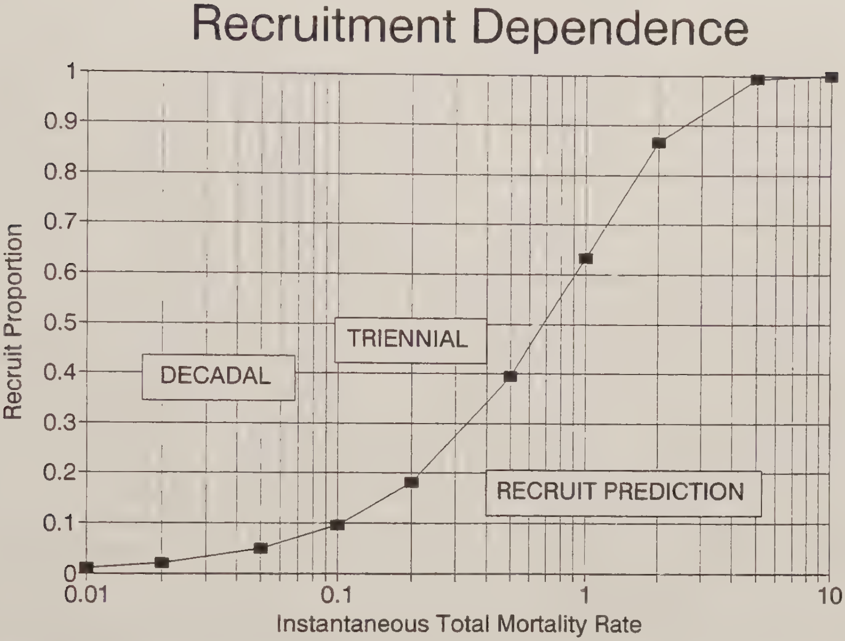

Figure 1. Relationship among population characteristics, intensity of fishery, and management biomass assessment practices. Instantaneous total mortality is the sum of natural mortality, mortality caused by other monitored species, and projected fishing mortality. The "decadal" scale is used for long lived species with smaller fisheries. The "triennial" scale is used for stocks with shorter life spans. The "prediction" scale is for recruitment prediction of stocks.

## Frequency of Estimate

As the fishery management process matures, dozens of stocks will be fished and additional species may also have to be monitored for fisheries impact: the cost of providing annual estimates of the health of all populations may be prohibitive. It could be determined, for each population, what interval is tolerable between estimates of population size. Empirical and simulation techniques (Reddingius and den Boer, 1970; Garrod and Knight, 1979) exist for determining the time course of a population change. As an example one could establish regions on a graph of ITMR versus recruitment rate as in Figure 1. For instance if the ITMR is below 0.1, one may need no more than a single biomass estimate to establish the population level on an absolute basis and thereafter relative measures of population growth and decline could be sufficient. One could envision that absolute measures of biomass could be on the decadal scale in that case. On the other hand, if the ITMR is above 1.0, more than 60% of each year's catch would be from recruits, no existing monitoring method might be sufficient: recruitment prediction methods would need to be developed.

## Population Areal Distribution

MacCall (1990) has discussed the interactions among population size, population density, and population area. For Pacific sardine and northern anchovy, these relationships had also been shown by Ahlstrom (1967). One of the dangers of managing fish using catch per unit effort (CPUE) is that this measure, at best, estimates a local population density in the fishing area. It seems likely that catch per unit effort data could be usefully augmented by a measure of spawning area during a fishery. If a fishing moratorium were in place, the spawning area, by itself, could provide a useful measure of the stock size. This practice was initiated by Wolf and Smith (1985) for the sardine moratorium following the apparent low level recovery of the stock (Wolf and Smith, 1986; Wolf et al., 1987). A theoretical basis for the decision to use area-based or spawning-rate-based biomass estimation methods was discussed by Mangel and Smith (1990).

The primary reason an area-based estimate of sardine biomass works relatively well is that the quantitative methods work so badly. Most of the eggs are deposited in a small area, possibly as a sperm-conservation tactic: with a small number of observations, it is unlikely to encounter the primary concentration and, when encountered, the rare sample appears as an outlier (Smith, 1973). While the egg samples can be approximated by a log-normal distribution, the presence of the eggs is distributed as a binomial. As the eggs disperse, they soon cover most of the area where spawning fish have been in the past several days. A simulation of the egg distribution shows that a single sample has only a 22% chance of getting "0" eggs in the spawning area and five samples have only a 1% chance of missing all eggs (table 2 in Wolf and Smith, 1985). The same simulation shows that one must take 500 samples to obtain a standard error 30% of the mean. Further evidence on egg distribution and sampling error is contained in Smith and Hewitt (1985) and Jahn and Smith (1987). One caution is that bootstrapping techniques use the samples collected up to this time and later sampling will undoubtedly increase the upper limit of egg concentrations.

## CONCLUSION

Minimal measures need only to include monitoring the catch rates for certain long lived, lightly fished populations; some fisheries may become so intensive that no monitoring scheme is adequate to prevent over-fishing in a changeable environment. For these latter fisheries, it is necessary to develop recruitment predictions. To decide the preliminary approach to new fisheries or new levels of fishing on existing fisheries, one merely derives a crude estimate of the spawning biomass, natural mortality, and projected fishing mortality. If this indicates a low level of fishing and natural mortality (ITMR $< 0.1$) the population may need only a low level of monitoring effort, such as monitoring of spawning area or catch per unit of effort. Intermediate intensities of fishing ($0.1 <$ ITMR $< 0.4$) require accurate triennial biomass monitoring. If the ITMR is projected to be above 0.4, existing biomass monitoring procedures would not likely provide sufficient and timely information for management decisions. It is particularly critical that the skewed distribution of recruitment, essentially log-normally distributed (Hennemuth et al., 1980), be considered when setting management procedures and fishing mortality rates. For the most intensive levels of fishing mortality in variable habitats, recruitment prediction probably will be the only feasible way of managing fisheries. There are no direct measurements or acoustic survey procedures implemented for this purpose and the costs of development will be substantial.

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# STOCK ASSESSMENT OF NEHU, *ENCRASICHOLINA PURPUREA*, USING THE EGG PRODUCTION METHOD

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## ABSTRACT

Nehu, *Encrasicholina purpurea*, are short lived, tropical anchovies used as baitfish for the Hawaiian pole-and-line tuna fishery. The spawning biomass of nehu within Pearl Harbor, Hawaii, was estimated weekly using the Daily Egg Production Method (DEPM). Over the 2-year study period, spawning biomass varied between 0.5 and 5.0 metric tons in response to the intensive fishery and a seasonal cyclicity in reproductive effort.

Nehu, *Encrasicholina purpurea*, are among the smallest of anchovies, yet they are commercially valuable as the primary bait used by the Hawaiian pole-and-line fishery for skipjack tuna, *Katsuwonus pelamis* (Uchida, 1977). Similar to other stolephorid baitfishes (Dalzell, 1987), nehu are extremely short lived (<6 months; Struhsaker and Uchiyama, 1976) and spawn almost continuously throughout the year (Tester, 1952; Clarke, 1987, 1989). Unlike the others, nehu occur exclusively within estuarine embayments, migrating daily between diurnal resting areas along turbid shorelines and nocturnal spawning areas in relatively clear channels. The commercial fishery exploits this unusual behavior, and is thereby unique among baitfish fisheries, by using seines to capture nehu in their shallow daytime habitat (Uchida, 1977; Dalzell and Lewis, 1989).

Nehu abundance has fluctuated over time and occasionally has declined to such an extent that vessels have spent nearly as much time fishing for bait as for tuna. The economic hardships resulting from the periodic shortages of nehu precipitated early efforts at stock assessment using either egg and larva data (Tester, 1951, 1952) or commercial catch statistics (Bachman, 1963), but for a variety of reasons, both approaches were not totally successful (Wetherall, 1977; Clarke, 1987). However, a new approach to stock assessment has recently been developed that is particularly suitable for pelagic, schooling species such as nehu.

The new approach, known as the Daily Egg Production Method (DEPM), is especially effective for schooling fishes because it utilizes information from the life-history stage that is the easiest to sample: the egg stage. The underlying premise of the DEPM is that the daily production of eggs by the stock is proportional to its spawning biomass. This concept, which was originally formulated by Saville (1964) and later elaborated by Parker (1980) and Picquelle and Stauffer (1985), can be expressed:

$$B = P/FR \qquad (1)$$

where B is the biomass, P is the daily production of eggs by the population, F is the batch fecundity per gram body weight of spawning females, and R is the proportion, by weight, of spawning females in the population. Definition of the population, and therefore the calculation of R, can be in terms of mature fish (spawning stock) or fish larger than some minimum size (commercial stock). In practice, P is estimated by sampling pelagic eggs with a plankton net, and F and R are estimated by sampling adult fish.

In this paper, the DEPM is used to assess the size of the nehu population occurring within Pearl Harbor, Oahu, which supports the second most important baitfish fishery in the Hawaiian Islands. Compared to previous applications on such temperate species as anchoveta, *Engraulis ringens* (Alheit, 1985), and northern anchovy, *E. mordax* (Lasker, 1985), assessments were conducted frequently to capture the rapid population fluctuations produced by nehu's inherently high turnover rate and the occasionally intensive fishery. High-frequency sampling and several design modifications resulted in an approach which differed in some respects form the established approach for DEPM (Lasker, 1985). These differences will be emphasized herein.

## Materials and Methods

Pearl Harbor was sampled on 1 day each week from 3 April 1986 to 7 April 1988. Each sampling day was separated into two periods: planktonic egg sampling and adult sampling. Eggs were sampled between 0900 and 1200 with a systematic sampling design (Cochran, 1963) in which a single sample was taken sequentially near the geographic center of each of 39 strata (Fig. 1). The net used measured 5 m long and 1 m in diameter at the mouth and was constructed of 335-$\mu$m Nitex. To allow its use from small boats, the net was not towed and instead was simply thrown overboard and allowed to sample as it descended to the bottom (average depth, about 12 m). Compared to a typical towed plankton net, our sampling net had two design features added to increase its effectiveness for this mode of operation. First, to increase the sinking speed, 5 kg of lead weights were attached to the steel ring that held the mouth open. Second, to ensure closure, the retrieval line was attached to a choke collar surrounding the net. Mesh bags of 335-$\mu$m Nitex were used as cod ends. When retrieved, these bags were sealed and placed in a 10% buffered formaldehyde solution.

In the laboratory, the plankton samples were examined without subsampling, and all nehu eggs were counted without developmental staging. Egg density at each station was estimated by dividing the egg count by an estimate of the filtered volume. Filtration volume was computed as water depth multiplied by the mouth area of the net.

Adult nehu were sampled in a 1.5-h period preceding sunset when the eggs to be spawned that evening were sufficiently hydrated to allow pre-spawning females to be unambiguously distinguished from non-spawning females (Clarke, 1987). Adults, along with juveniles, were captured by a beach seine with the same mesh size (9 mm) and design characteristics as a commercial nehu seine, except that it was cut to approximately one-third scale (70 m long by 3 m deep) so that it could be set from a small boat. Nehu schools were located in their daytime habitat, with the same searching techniques used by commercial vessels. When found, schools were quickly surrounded with the seine, and a random sample of the catch was taken and immediately preserved in a 10% buffered formaldehyde solution.

In the laboratory, a subsample of nehu was drawn from each field sample: 1) An initial subsample of approximately 50 fish was randomly chosen. 2) In order of size, starting with the apparently largest individual, fish were removed from the subsample and examined microscopically for sex and stage of maturity. 3) If less than 25 mature females were obtained from the initial subsample, additional subsamples were drawn and examined completely in the same manner until at least 25 mature females were obtained. 4) To increase the speed of classifying fish, if six juveniles were drawn in succession from a subsample, all of the remaining fish in that subsample were also classified as juveniles without examination.

The criteria used to classify fish were based upon the following gross morphological features partly adapted from Clarke (1987): 1) largest ova $\geq 0.7$ mm long indicated a mature female with hydrated eggs; 2) largest ova 0.5 to 0.7 mm long indicated a mature female with unhydrated eggs; 3) testis depth (dorsal-ventral) greater than or equal to eye diameter indicated a mature male; 4) largest ova $<0.5$ mm long or testis depth of less than eye diameter indicated a juvenile.

After the subsample was chosen and classified, the following biological attributes were measured. Standard length (in mm) was measured for all mature fish and for the first 25 randomly chosen juveniles; any remaining juveniles were counted but not measured. All fish measured for length (except females with hydrating eggs) were measured for total body weight (in mg) after being blotted dry; ovary-free body weight was measured for all females. Batch fecundity was estimated for females with hydrating eggs by teasing both ovaries apart and counting under a microscope all hydrating ova. Each count was replicated, and fecundity was estimated as the mean of the two counts. Over the 105 consecutive weeks of sampling, this process was repeated for each of 162 seine samples.

Samples of nehu were also obtained from commercial vessels baitfish fishing in Pearl Harbor during the study period. The methods of collecting these samples varied because the samples were taken by the fishermen themselves, but the general procedure consisted of scooping 100 to 200 fish from the bait well and temporarily preserving them with salt and ice until fishing was completed and they could be frozen. Frozen fish were later fixed in a 10% buffered formaldehyde solution. In the laboratory, up to 100 of the fish were randomly removed from each sample and measured for standard length (in mm). A total of 36 commercial samples was collected.

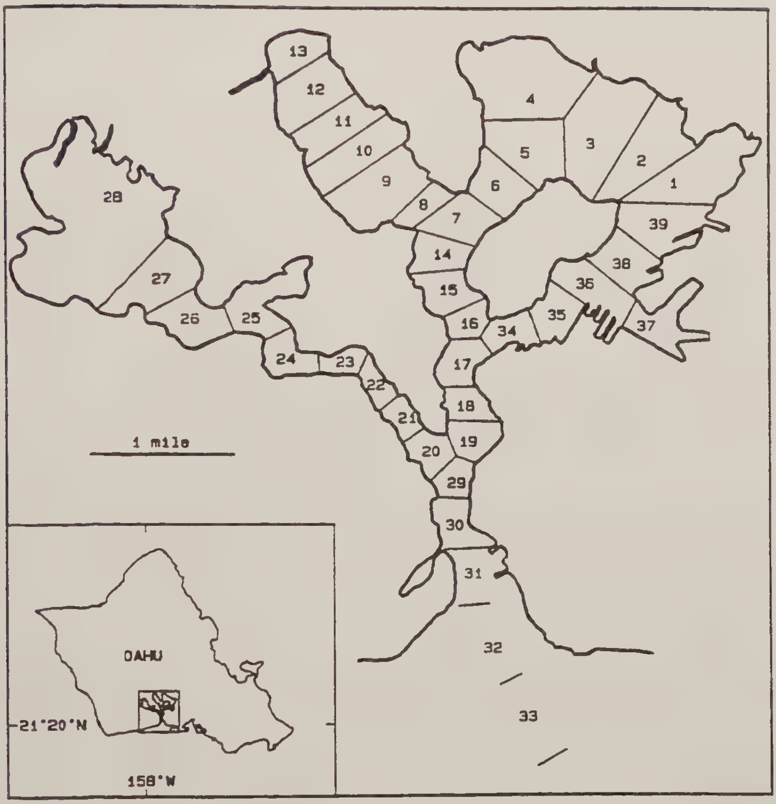

Figure 1. Locations of the 39 sampling sites in Pearl Harbor, Oahu.

*Data Analysis and Weekly Biomass Estimation.*—Evaluation of Equation 1 requires estimates of P, F, and R. These estimates were obtained as follows. Daily egg production was estimated as

$$P = \sum D_i V_i \tag{2}$$

where $D_i$ is the estimated egg density (eggs per volume filtered) and $V_i$ is the volume of the ith stratum. Strata volumes were estimated as the surface areas measured on a navigation chart times the average sounding depth. The summation is over all 39 strata. Relative fecundity was estimated from each sample as

$$F = \sum E \Big/ \sum W_{fh} \tag{3}$$

where $\Sigma$ E is the sum of all hydrating ova, and $\Sigma W_{fh}$ is the sum of the corrected total body weight of mature females with hydrating eggs. Spawning proportion was estimated from each sample as

$$R = \sum W_{fh} \Big/ \left(\sum W_m + \sum W_{fh} + \sum W_{fu}\right) \tag{4}$$

where $\Sigma W_m$ and $\Sigma W_{fu}$ are the sums of the total body weights of males and of females with unhydrated eggs. The $W_{fh}$ values were corrected for the temporary weight gain due to egg hydration by regression $W_{fu}$ on ovary-free weight for females with unhydrated ovaries, then predicting $W_{fh}$ from the ovary-free body weights of females with hydrated ovaries.

Since the commercial catch includes juveniles, the commercial population will be larger than the spawning population. To estimate the size of the commercial population, the methods used for research sampling were assumed to be so similar to those used by the fishery that the same size ranges were captured. Therefore when the commercial, rather than the spawning, population was estimated, Equation 4 was modified slightly to include in the denominator the term $\Sigma W_j$ or the sum of the total body weights of juveniles.

Variance and bias of the estimated biomass for each week were approximated by using the delta method (Seber, 1973; Parker, 1980). The variance estimator was

$$\mathrm{Var}(B) = B^2(\mathrm{CV}(P)^2 + \mathrm{CV}(F)^2 + \mathrm{CV}(R)^2 - 2\mathrm{Cov}(P, F)/PF \\ - 2\mathrm{Cov}(P, R)/PR + 2\mathrm{Cov}(F, R)/FR) \tag{5}$$

and the bias estimator was

$$\mathrm{bias}(B) = B(\mathrm{CV}(F)^2 + \mathrm{CV}(R)^2 + \mathrm{Cov}(F, R)/FR) \tag{6}$$

where CV represents the coefficient of variation, and Cov represents the covariance. For both the variance and bias equations, the covariance terms were considered negligible and therefore were omitted.

The variances needed to evaluate Equations 5 and 6 were estimated as follows. The variance of P was estimated as

$$\mathrm{Var}(P) = \sum V_i^2 \mathrm{Var}(D_i) \tag{7}$$

where $\mathrm{Var}(D_i)$ was approximated as the variance in $D_i$ among three adjacent stations, because the plankton net samples were not replicated at each station. The variances of R and F were estimated as

$$\mathrm{Var}(\bar{X}) = \sum (X_i - \bar{X})^2/N(N - 1) \tag{8}$$

where $X_i$ is the ith estimated value of R or F, and $\bar{X}$ is the mean of N values of R or F. Since the number of samples collected each week was always small and sometimes even insufficient to estimate variance, the weekly estimates of the means and variances of the biological parameters were calculated from a pool of all samples within a 5-week moving time window centered on a particular week. Weekly estimates of egg production, which were based on much larger sample sizes, were not smoothed in this manner.

To test whether the nehu length distribution of the research catches differed from that of the commercial catches, the following three steps were taken. First, all commercial length samples and all research length samples taken within each week were pooled. Second, equality of the commercial and research length-frequency distributions for each week was tested by a two-tailed Smirnov test (Conover, 1971). Third, the probabilities associated with the individual weekly tests were combined over all sampling weeks using procedures described in Sokol and Rohlf (1981: 779).

To test whether nehu school according to sex and maturity stage, the number of pre-spawning females in each seine sample was compared to the number of non-spawning females, the number of males was compared to the number of females, and the number of mature fish was compared to the number of juveniles. In each of three cases, a test was made by using a chi-square test of heterogeneity (Sokol and Rohlf, 1981) over all 162 adult samples. To minimize the effect of temporal changes in spawning proportion or sex ratio on the test, expected values were computed from the monthly means rather than the overall mean.

## RESULTS AND DISCUSSION

Weekly estimates of spawning and commercial biomass (Fig. 2) had similar patterns of variation over time, but commercial biomasses were considerably larger and had wider confidence intervals. The three components of the biomass estimates (i.e., daily egg production (P), proportion spawning (R), and relative fecundity (F) also displayed patterns in their temporal variation (Fig. 3). For P, the pattern is similar to that of biomass and indicates that the biomass estimates are primarily determined by egg production. For R and F, the pattern is largely seasonal although R also displays a shorter period of variation as well as a linear trend. Examined below are aspects of the sampling design that could have led to possible uncorrected bias in these estimates or were strongly influential in determining precision.

Bias in the biomass estimates is a function of bias in P, R, and F in addition to the bias from Equation 6. Egg production could be influenced by three potential sources of bias. First, egg production could be overestimated if the counts of nehu eggs included eggs of other species or included nehu eggs spawned on other nights.

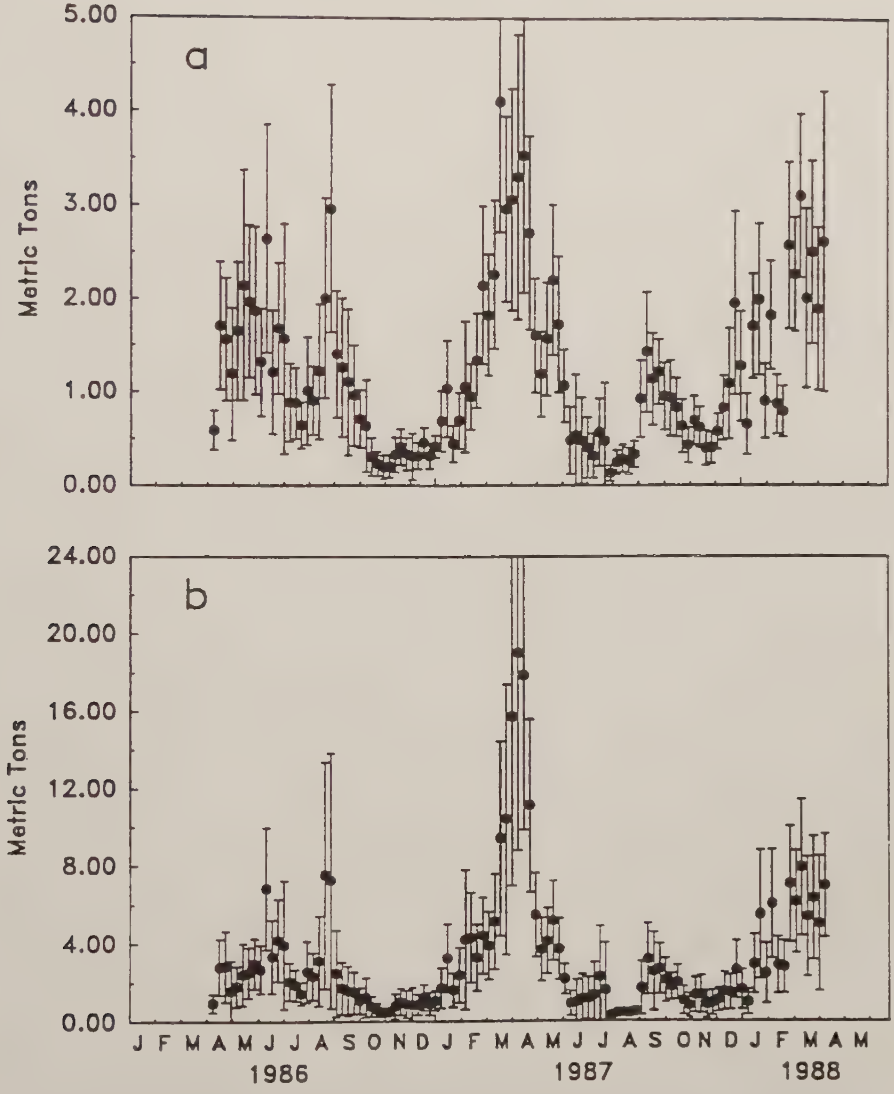

Figure 2. Weekly estimates and 95% confidence intervals of the (a) spawning and (b) commercial biomasses of nehu within Pearl Harbor.

Misidentification, however, is unlikely because no other fishes in Pearl Harbor have eggs similar to those of nehu (Tester, 1951; Clarke, 1987), and inclusion of multiple cohorts in the egg counts is unlikely because nehu eggs usually hatch within 24 h (Clarke, 1987). Second, egg production could be underestimated if egg mortality over the period between spawning and sampling is actually large. Unfortunately, our sampling design was insufficient to allow estimation of egg mortality, and likely values must be estimated indirectly. If the egg mortality rate

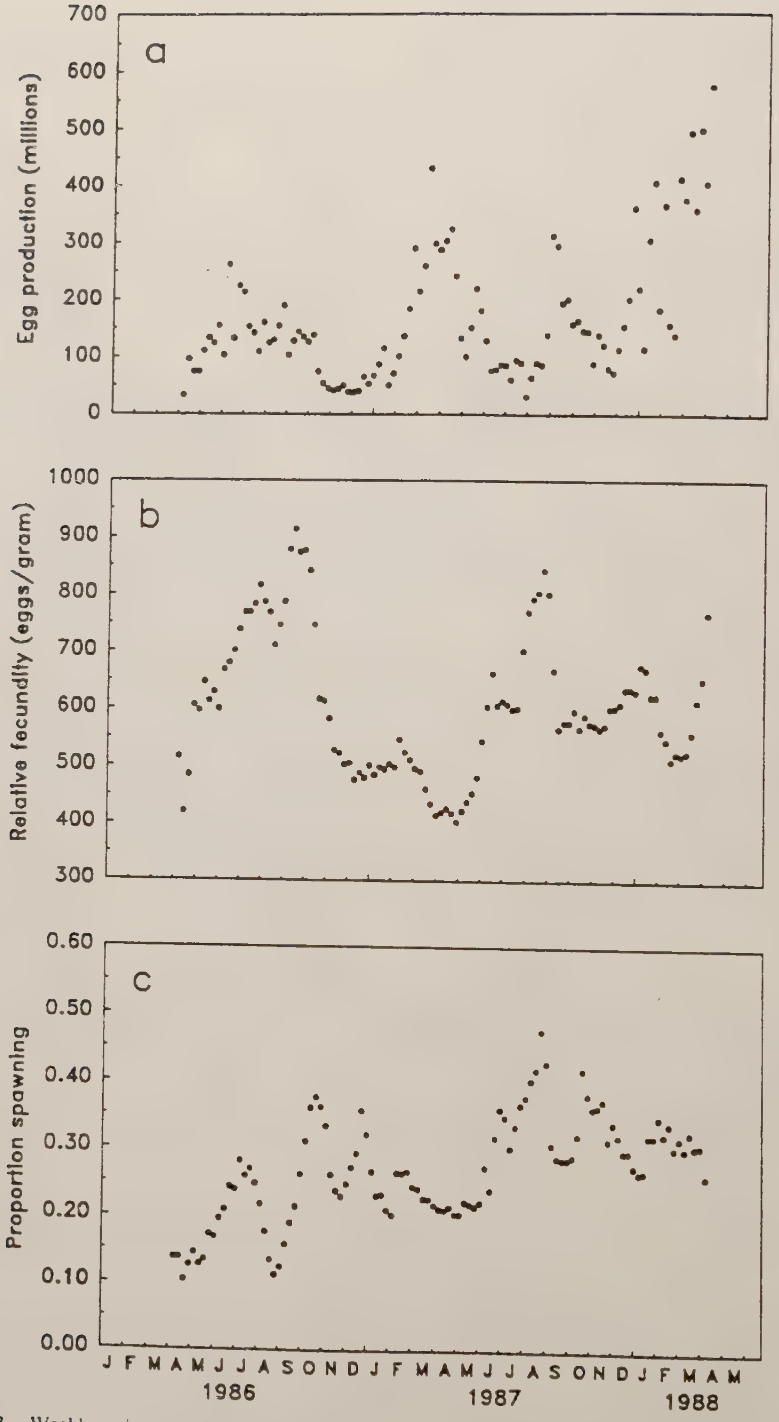

Figure 3. Weekly estimates of (a) daily egg production, (b) relative fecundity, and (c) proportion, by weight, of spawning females in the spawning population.

is the same as it is for northern anchovy (25% per day; Lo, 1986), then approximately 15% of nehu eggs would die during the 16-h period between spawning and sampling (nehu spawn in a 2-h period after sunset; Clarke, 1987). However egg mortality may be considerably less than this because 68% of northern anchovy egg mortality is due to egg cannibalism (based on data from Hunter and Kimbrell, 1980) and nehu rarely cannibalize their eggs (Hiatt, 1951).

Third, egg production estimates could be biased because of a corresponding bias in the estimates of strata volumes. Unlike previous studies on oceanic anchovies (e.g., Picquelle and Stauffer, 1985), egg density was specified in terms of water volume rather than surface area, because nehu eggs are distributed throughout the water column and water depth varies within Pearl Harbor. Strata volumes were measured crudely using a navigation chart and could be considerably biased.

Proportion spawning and relative fecundity are likewise subject to several types of bias. Proportion spawning could be underestimated if pre-spawning females were misidentified. Since pre-spawning females were identified by egg size, sampling had to be restricted to a time of day that the hydrating ova were sufficiently enlarged to be unambiguously distinguishable from unhydrated ova. Previous research (Clarke, 1987) indicated that ova hydrate during the later afternoon, but not until 2 h before sunset do all pre-spawning females have some enlarged ($\geq 0.7$ mm) ova. Because of the importance of correct timing, we repeated part of Clarke's (1987) study by sampling nehu at approximately half-hour intervals in the late afternoon. On the basis of these samples, we shortened the sampling period to 1.5 h before sunset to ensure correct identification. Although we believe that nearly all pre-spawning females were correctly identified, some of the hydrating ova within these females may not have been recognized because of size variability among hydrating ova in the early part of the period. If so, an occasional underestimate of relative fecundity could have resulted.

Proportion spawning could be biased if pre-spawning and non-spawning females segregate spatially and become differentially available to the sampling gear. For anchoveta (Alheit, 1985) and northern anchovy (Picquelle and Stauffer, 1985), pre-spawning females near the time of spawning segregate from non-spawning females, aggregate with males, and have a higher vulnerability to the sampling gear, perhaps because of a difference either in net avoidance or in depth distribution. Evidence that nehu were similarly segregated during the sampling period was provided by the chi-square tests of heterogeneity in the relative abundance of pre-spawning females to non-spawning females, females to males, and adults to juveniles, which were all highly significant ($P < 0.001$). Although such segregation increases biological heterogeneity among schools and thereby increases the variance in the estimates of proportion spawning, it leads to bias only when the segregated schools are differentially vulnerable. Pre-spawning and non-spawning nehu, however, are apparently equally vulnerable during the sampling period because our overall estimate of the mean proportion spawning based on numbers of mature females, rather than population biomass (0.53), was not significantly different from Clarke's (1987) estimate of 0.50 based on postovulatory follicles and estimated rates of ova development from fish sampled at all times of the day.

Proportion spawning for the commercial population (Fig. 3c) could be biased if the size distribution of fish in the research samples differed from that in the commercial samples. Initially we believed that sampling nehu with the same mesh size as a commercial net ensured catching the same size range of fish. Since mesh size may not be the sole determinant of size selection with seines, we later became concerned that the longer, deeper seines used by the commercial fishery allowed the catch of larger fish. However, the length distributions of the nehu in com-

Table 1. The relative contribution of the error in each of three parameters—P (daily production of eggs by the population), R (proportion, by weight, of spawning females in the population), and F (batch fecundity per gram body weight of spawning females)—to the error in the biomass estimate. Unsmoothed estimates of $CV^2$ for R and F are averages over the 52 weeks having at least two fish samples. The largest covariance term in Equation 5 (Cov(F, R)/FR) is also shown for the smoothed estimates

| | $CV(P)^2$ | $CV(R)^2$ | $CV(F)^2$ | Cov(F, R)/FR |
|---|---|---|---|---|
| No smoothing | | | | |
| Spawning biomass | 0.032 | 0.081 | 0.014 | |
| Commercial biomass | 0.032 | 0.218 | 0.014 | |
| Smoothing | | | | |
| Spawning biomass | 0.032 | 0.030 | 0.007 | <0.001 |
| Commercial biomass | 0.032 | 0.066 | 0.007 | 0.015 |

mercial and research samples were not significantly different ($P > 0.05$), and sampling was therefore unbiased.

Variance of the biomass estimates is a function of the variances of P, R, and F. One convenient way of examining how the precision of each parameter contributes to the precision of the biomass estimate is to express precision in terms of $CV^2$ (Equation 5). When expressed in this way, the average of the weekly estimates of $CV(R)^2$ is considerably larger than $CV(F)^2$ and $CV(P)^2$ (Table 1), especially when the estimate of R includes the weight of juveniles, as it does in the calculation of commercial biomass. There are two reasons why precision in the biomass estimates is dominated by precision in the estimates of spawning proportion. First, the restricted period of fish sampling—bounded between the times of day when hydrating ova became clearly recognizable and when nehu leave the shallow nearshore area to begin spawning—was so short that few samples could be collected (an average of only 1.6 samples collected each week). Second, sampling occurred when pre-spawning and non-spawning fish were segregating in preparation for the evening spawning, and such segregation increases the between-sample variability in proportion spawning.

The covariance between P, F, and R was assumed to be negligible and therefore omitted from the estimated variance of the biomass estimates. As a check on the adequacy of this assumption, the covariance term for F and R (the largest of the three possible terms) was computed for the smoothed estimates of spawning and commercial biomasses (Table 1). For spawning biomass, the covariance term was less than 1% of the sum of the variance terms. For commercial biomass, however, the covariance term was about 14% of the sum of the variance terms and was not negligible. The larger covariance was due to the inclusion of juvenile weights in the computation of P as well as the variation in F with body size. Thus, when a school of small nehu is sampled, R will tend to be low because of the relatively high abundance of juveniles, and F will tend to be low because of the small size of mature females.

To obtain less variable estimates of the parameters and to fill gaps in the time series when insufficient samples were collected (about one-half of the weeks lacked the minimum two samples needed to calculate variance), proportion spawning and relative fecundity were estimated from all samples taken within a running 5-week interval centered on a specified week. Intervals of other widths (3, 7, 9, 11 weeks) were also examined, but 5 weeks was chosen as the best because the sum of the $CV(R)^2$ and $CV(F)^2$ terms was approximately equal to $CV(P)^2$. If proportion spawning and relative fecundity varied slowly with time, then such a smoothing procedure effectively increases sample size and thereby reduces variance of the estimates. Variation in response to short term events, however, would be lost.

One conspicuous difference between this study and previous applications of the DEPM is the spatial and temporal scales that were employed in the sampling design. For example, applications on anchoveta (Alheit, 1985) and northern anchovy (Lasker, 1985) considered populations distributed over thousands of square kilometers, whereas the nehu population was constrained to an enclosed area of $<10$ km$^2$ that could be sampled in a few hours from a small boat. This difference in spatial scale, and the difference in the rate of biological turnover, dictated the time scales of sampling; thus, nehu were sampled at weekly intervals. Frequent assessment, however, also required rapid processing and analysis of the field samples; this, in turn, required several modifications to the sampling procedures used in previous applications of the DEPM.

The most important modification was the use of hydrated ova rather than post-ovulatory follicles to identify spawning females. Although this approach was faster and easier because histological preparation was not required, it restricted sampling to a period that occurred when schools were segregating in preparation for spawning and was so brief that few samples could be collected. As a consequence, the variance of the weekly estimates of the reproductive parameters was sometimes not calculable and was always quite large. Temporal smoothing reduced these problems, but also reduced the independence of the weekly estimates of biomass. Regardless of this problem, the results of this study demonstrate that the DEPM can be successfully employed using small boats and hand-operated sampling gear to assess the biomass of small tropical species.

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# Relative abundance of pelagic resources utilized by the California purse-seine fishery: Results of an airborne monitoring program, 1962–90

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**Abstract.** – During the period 1962–90, an aerial monitoring program conducted in cooperation with aerial spotters searching for pelagic fishes off California and Baja California, Mexico resulted in the development of an index of apparent abundance for six species of fishes: the northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, Pacific bonito *Sarda chiliensis*, Chub mackerel *Scomber japonicus*, jack mackerel *Trachurus symmetricus*, and bluefin tuna *Thunnus thynnus*. Northern anchovy was the dominant species observed, accounting for 89.7% of tonnage recorded during 1962–90. Chub mackerel comprised 6.1% of the total tonnage, jack mackerel 2.1%, Pacific sardine 1.0%, Pacific bonito 0.6%, and bluefin tuna 0.5%.

Apparent abundance indices were computed by dividing the tonnage observed by the number of "block areas" (10' lat. × 10" long.) searched, expressed as tons/block area flown (T/BAF). Indices were calculated for the total area and for the core area of distribution and abundance for each species. All species exhibited large fluctuations in apparent abundance over time. The apparent abundance index for Pacific sardine declined to a very low level during 1966–83. A substantial increase in abundance occurred during the mid- to late-1980s, with the 1990 index value 58 times that observed during the early 1960s. The chub mackerel abundance index declined to a very low level during 1966–76, then increased to a record high value in 1978 and has since declined. The northern anchovy abundance index increased in the early 1970s, with high abundance levels recorded during 1972–81, and then declined sharply to very low levels in the 1980s. The Pacific bonito abundance index was high during 1965–67 and 1983–85, with current levels well below the long-term mean. Very high abundance index levels for jack mackerel were recorded during 1975–79, then declining to very low levels in the 1980s. The bluefin tuna abundance index increased during 1972–80, declining to very low index values since. Based on these data, several species appear to be fluctuating unpredictably with respect to species abundance over time.

Aerial indices were compared with available total, spawning, and larval biomass estimates developed for several species. The most significant correlation of the aerial index was between the northern anchovy and Pacific sardine larval indices.

The rapid decline of the Pacific sardine *Sardinops sagax* fishery in the late 1940s resulted in increased research by the State of California Department of Fish and Game (CDF&G), Federal Government, and other institutions to determine the underlying principles that govern the sardine's behavior, availability to the fishery, and total abundance (Clark & Marr 1955, Sette 1969, Radovich 1982). Catch-per-unit-effort (CPUE) studies of the sardine purse-seine fishery off California did not indicate a significant decline in abundance until just prior to the fishery collapse (Fox 1974). Fisheries tend to target their fishing effort in areas of high densities of fishes (Radovich 1982, Squire & Au 1990), hence CPUE may not accurately reflect resource abundance (de La Mare 1984; J.B. Phillips, CDF&G, pers. commun., 1954). Clark & Marr (1955) concluded that, in addition to other information needs, better information is needed on changes in availability of sardine to the fishery. Related to this is the need for better real-time measures of trends in apparent abundance for successful management of pelagic schooling resources.

In the mid-1950s, the use of aircraft in searching and fishing operations of the California purse-seine fleet had become well established, as was the case in many other U.S. fisheries (Squire 1961). Having had experience in conducting commercial aerial fish spotting and several aerial fish-resource surveys, I initiated a pelagic monitoring program in the fall of 1962, with the cooperation of aerial fish-spotter pilots searching for fish for the commercial purse-seine fishery off central and southern California. The purpose of the program was to develop an effective method of measuring apparent abundance and monitoring changes in abundance. In the case of aerial observations, the concentrations of fish observed may or may not be subjected to fishing.

This paper updates the analysis of apparent abundance data collected by the aerial monitoring program from the first full year of data, 1963–90, using different analytical methods than used in earlier papers (Squire 1972, 1983). It also reviews the trends in apparent abundance during the period 1963–90 for six pelagic species by geographical area and compares the relation of the aerial abundance estimates to other independent biomass estimates made for the same species. The term "apparent abundance" (Marr 1951) refers to that portion of total abundance that is available to the fishery.

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Species included in this study are the northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, Pacific bonito *Sarda chiliensis*, chub mackerel *Scomber japonicus*, jack mackerel *Trachurus symmetricus*, and bluefin tuna *Thunnus thynnus*. These species, along with market squid *Loligo opalescens*, are the primary targets of the commercial purse-seine fleet based in San Pedro, California. Most are also fished by the southern California sportfishing fleet. The species are members of a complex interacting coastal and oceanic ecosystem that crosses international boundaries (Sette 1969).

## Methods

### Procedures for collection and tabulation of data

Since the fall of 1962, fish-spotter pilots have been directed to complete a flight logchart at the termination of each spotting flight. These pilots were instructed to draw their flight track on the chart and record the locations of all schools of fish species observed, along with their best estimates of tonnage observed. These data were recorded either as total tonnage of fish in

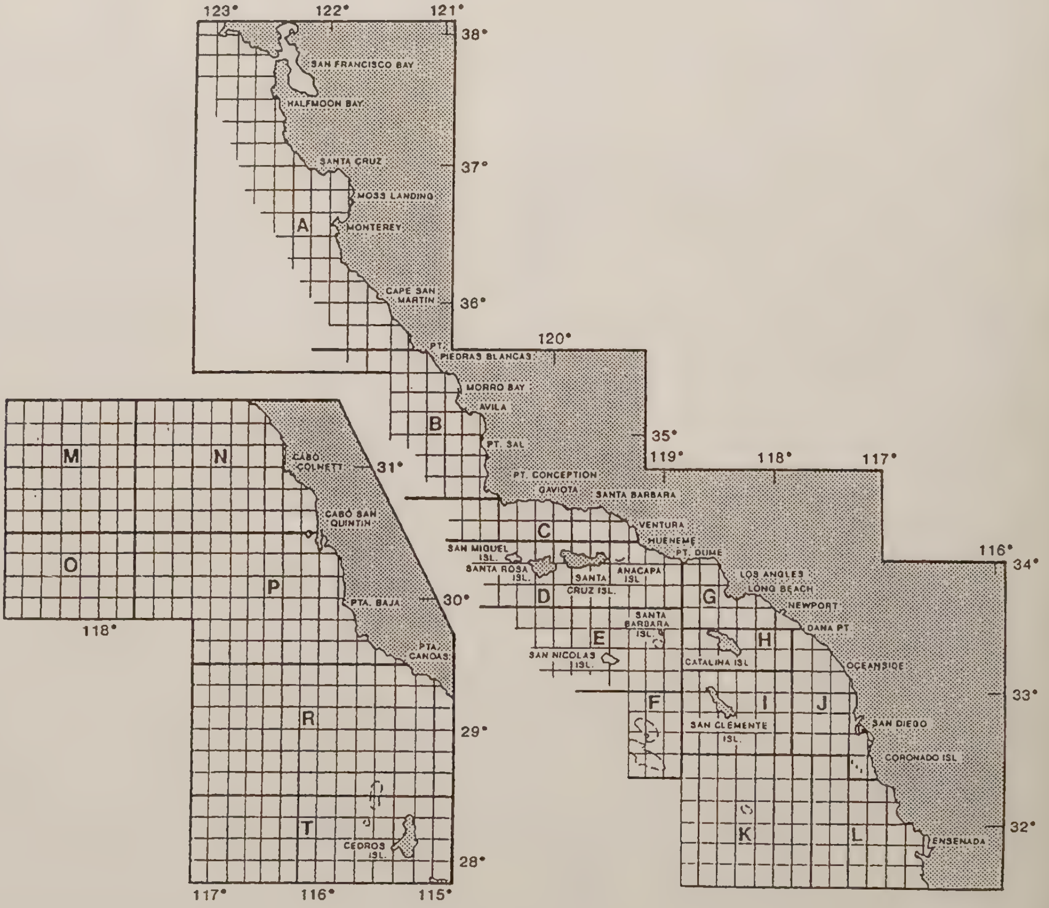
123°
122°
121°
38°
SAN FRANCISCO BAY
HALFMOON BAY
SANTA CRUZ
37°
MOSS LANDING
A
MONTEREY
CAPE SAN MARTIN
36°
120°
PT. PIEDRAS BLANCAS
MORRO BAY
AVILA
B
35°
PT. SAL
119°
118°
117°
PT. CONCEPTION
GAVIOTA
SANTA BARBARA
C
VENTURA
HUENEME
PT. DUME
116°
34°
SAN MIGUEL ISL.
SANTA ROSA ISL.
SANTA CRUZ ISL.
ANACAPA ISL
LOS ANGLES
LONG BEACH
NEWPORT
D
G
SANTA BARBARA ISL.
DANA PT.
E
H
SAN NICOLAS ISL.
CATALINA ISL
OCEANSIDE
33°
F
I
J
SAN CLEMENTE ISL.
SAN DIEGO
CORONADO ISL
K
L
32°
ENSENADA
M
N
CABO COLNETT
31°
CABO SAN QUINTIN
O
P
PTA. BAJA
30°
118°
PTA. CANOAS
R
29°
T
CEDROS ISL.
28°
117°
116°
115°

**Figure 1**

Block areas designated for sampling from off central California to Mexico, grouped in 18 zones, A to T. (Zones Q and S were originally used on flight logs; however, no flights were recorded for these zones.)

the area or numbers of schools with an estimate of the tonnage of each school. Procedures for recording species observations and survey effort have not changed since 1962. Other information such as time of flight (day or night) and flight duration also are recorded on the flight log. Flight logs are submitted quarterly and data from each log are entered into the computer after editing.

Spotter pilots' income is derived from the commercial fishery at a current rate of ~6% of the vessel's gross income. Spotter pilots are paid a nominal fee by the National Marine Fisheries Service (NMFS) to maintain a flight log record of their observations. Pilots in the program averaged ~600h flight time/yr and, with 4–6 pilots, the total number of hours flown was ~3000/yr.

From 1963, the first full year of operation, to 1990, annual indices of abundance for each species were calculated for the total area (from northern Baja California, Mexico to San Francisco, California) and for selected groups of 10' lat. × 10' long. block areas, similar to the "block area" statistical system used by CDF&G (Anon. 1935). These groups of block areas are referred to in this paper as "zones" and were designed to encompass important commercial fishing areas (Fig. 1).

Flight effort for the total area and each zone was determined by counting the number of times the aerial spotter's flight track entered a block area, termed a "block area flight" (BAF). Species abundance was recorded as the tonnage estimate (and hence approximates biomass) for the area observed. Also recorded on the flight log was time of the observation (day or night), pilot, and, since 1988, the target species of the commercial operation.

The procedure to measure effort has not changed from previous studies; however, the computation of species abundance has been modified. In previous analyses (Squire 1972, 1983), abundance was estimated as a rank index according to discrete incremental values of tonnage (tonnage range values). For example, for the northern anchovy, an observation within a block area estimated to be 0–100t was recorded as 1, 100–200t was recorded as 2, etc. Each species had different tonnage range values, since the amount of tonnage observed varied greatly between species. Therefore, the abundance index values for each species are not directly comparable. For this analysis, actual tonnage values as recorded by the spotter pilot and a modification of the index used by Squire (1972) are used, which allows for direct comparison of abundance index values between species.

The apparent abundance index is T/BAF, where T = tonnage estimate, and BAF = total number of block area flights (day plus night, all zones).

## Results and discussion

### Observation effort and sightings

During the period 1963–90, a total of 24 aerial fish-spotter pilots participated in the program and reported flight operations totaling over 67,000h, searching a total of 376,446 block areas. Table 1 gives the annual search effort (BAF/yr), day and night, during the period 1962–90. From 1963 to 1990, a total of 253,239 BAF were made during day operations (67%) and 123,207 BAF during the night. Pilots have searched an average of 13,444 BAF/yr; however, the variation in annual spotting effort is considerable. There was reduced effort in early 1970. Abundance data for 1970

**Table 1**

Search effort in block area flights (BAF), day and night, 1963–90, from off Baja California, Mexico to central California. Asterisk indicates <1/2 yr of operation.

| | Block area flights | | |
|---|---|---|---|
| Year | Day | Night | Total |
| 1962* | 362 | 512 | 874 |
| 1963 | 3,541 | 3,279 | 6,820 |
| 1964 | 5,245 | 3,415 | 8,660 |
| 1965 | 5,086 | 4,367 | 9,453 |
| 1966 | 7,708 | 3,781 | 11,489 |
| 1967 | 7,632 | 3,495 | 11,127 |
| 1968 | 7,823 | 3,835 | 11,658 |
| 1969 | 9,745 | 5,896 | 15,641 |
| 1970 | 4,646 | 1,853 | 6,499 |
| 1971 | 12,308 | 5,181 | 17,489 |
| 1972 | 7,402 | 4,448 | 11,850 |
| 1973 | 12,450 | 5,031 | 17,481 |
| 1974 | 8,356 | 3,887 | 12,243 |
| 1975 | 7,923 | 3,398 | 11,321 |
| 1976 | 14,782 | 3,781 | 18,563 |
| 1977 | 7,795 | 7,788 | 15,583 |
| 1978 | 6,517 | 4,415 | 10,932 |
| 1979 | 10,727 | 4,767 | 15,494 |
| 1980 | 3,624 | 3,403 | 7,027 |
| 1981 | 9,237 | 3,781 | 13,018 |
| 1982 | 9,597 | 5,754 | 15,351 |
| 1983 | 13,904 | 4,571 | 18,475 |
| 1984 | 9,144 | 1,063 | 10,207 |
| 1985 | 15,243 | 4,031 | 19,274 |
| 1986 | 12,300 | 5,684 | 17,984 |
| 1987 | 8,474 | 6,348 | 14,822 |
| 1988 | 7,185 | 3,335 | 10,520 |
| 1989 | 8,744 | 4,116 | 12,860 |
| 1990 | 16,101 | 8,504 | 24,605 |
| Total 1963–90 | 253,239<br>= 67% | 123,207<br>= 33% | 376,446 |

Avg. = 13,444 BAF/yr, 1963–90

### Table 2

Sighting estimates of total tonnage by species and percentage and by zones, for the period 1962–90.

| Zone | Northern anchovy | Pacific sardine | Pacific bonito | Chub mackerel | Jack mackerel | Bluefin tuna |
|---|---|---|---|---|---|---|
| A | 25,147,498 | 19,157 | 674 | 108,345 | 56,158 | 0 |
| B | 865,308 | 2,739 | 4,690 | 216,873 | 98,035 | 0 |
| C | 11,633,297 | *614,595* | *233,330* | *1,386,548* | 104,949 | 333 |
| D | 5,126,158 | 345,360 | 86,860 | 639,099 | 268,823 | 1,938 |
| E | 467,400 | 22,454 | 3,688 | 203,190 | 45,937 | 2,934 |
| F | 358,614 | 50,130 | 250 | 701,416 | *789,877* | 22,773 |
| G | *28,519,793* | 99,587 | 37,176 | 521,732 | 361,180 | 3,154 |
| H | 5,292,980 | 183,500 | 26,363 | 1,145,839 | 222,005 | 1,785 |
| I | 1,578,398 | 33,165 | 26,231 | 1,292,866 | 256,731 | 27,938 |
| J | 10,453,074 | 68,243 | 205,553 | 130,471 | 30,855 | 26,494 |
| K | 242,164 | 1,200 | 2,045 | 525 | 910 | 79,846 |
| L | 1,215,269 | 0 | 28,418 | 1,365 | 50 | 86,521 |
| M | 500 | 0 | 0 | 0 | 0 | 9,603 |
| N | 2,495,734 | 4,200 | 13,881 | 24,650 | 0 | *143,625* |
| O | 0 | 0 | 0 | 0 | 0 | 0 |
| P | 123,305 | 0 | 2,313 | 400 | 0 | 64,423 |
| R | 1,110 | 0 | 0 | 0 | 0 | 8,652 |
| T | 0 | 0 | 0 | 0 | 0 | 0 |
| | 93,520,602 | 1,444,321 | 671,472 | 6,373,169 | 2,235,510 | 480,019 |
| % | 89.7 | 1.0 | 0.6 | 6.1 | 2.1 | 0.5 |

### Table 3

Day/night sighting estimates for northern anchovy, Pacific sardine, Pacific bonito, Pacific mackerel, jack mackerel and bluefin tuna, 1962–90.

| | Day | Night |
|---|---|---|
| **Northern anchovy *Engraulis mordax*** | | |
| Tonnage | 30,140,974 | 63,379,618 |
| % day/night | 32.3 | 67.7 |
| **Pacific sardine *Sardinops sagax*** | | |
| Tonnage | 361,548 | 1,082,498 |
| % day/night | 25.1 | 74.9 |
| **Pacific bonito *Sarda chiliensis*** | | |
| Tonnage | 521,302 | 151,169 |
| % day/night | 77.5 | 22.5 |
| **Pacific mackerel *Scomber japonicus*** | | |
| Tonnage | 2,534,780 | 3,837,366 |
| % day/night | 39.8 | 60.2 |
| **Jack mackerel *Trachurus symmetricus*** | | |
| Tonnage | 746,827 | 1,488,683 |
| % day/night | 33.5 | 66.5 |
| **Bluefin tuna *Thunnus thynnus*** | | |
| Tonnage | 462,262 | 17,756 |
| % day/night | 96.3 | 3.7 |

are thus not directly comparable to other years, although most search effort was during a period of high abundance levels. Through the years, the center of search effort was off southern California, with search activity off northwestern Baja California, Mexico during the summer for bluefin tuna. There was considerable search effort north of Point Conception into the Monterey Bay area for chub mackerel and Pacific sardine during the early years of the program and less so since the decline in those species' abundances in the mid-1960s.

Estimates of total tonnage sighted by species by zone are given in Table 2. The tonnage estimated for northern anchovy far exceeds that of all other species, totaling 89.7%. The greatest tonnage of northern anchovy was observed in zone G; Pacific sardine, Pacific bonito, and chub mackerel in zone C; jack mackerel in zone F; and bluefin tuna in zone N.

Most spotting effort was carried out during summer to fall, with 49% of BAFs accounted for during the months of July, August, and September (1980–90). During any one year, the amount of effort expended in any one month was highly variable due to fluctuations in abundance, weather, and fleet operations. In summer months, a substantial portion of the increase in spotting effort is related to searching for bluefin tuna, or other species such as albacore *Thunnus alalunga* and yellowfin tuna *Thunnus albacares*.

Differences in tonnage sighted between day and night (Table 3) are similar to that reported by Squire (1972). Northern anchovy, Pacific sardine, chub mackerel, and jack mackerel were more commonly observed at night, while Pacific bonito and bluefin tuna were more commonly observed during the day.

## Table 4

Total area index values in T/BAF, day plus night. Dash indicates an abundance level <0.01 T/BAF.

| Year | Total area | Year | Total area |
|---|---|---|---|
| **Northern anchovy *Engraulis mordax*** | | | |
| 1962 | 0.66 | 1977 | 713.80 |
| 1963 | 141.38 | 1978 | 340.19 |
| 1964 | 80.66 | 1979 | 382.83 |
| 1965 | 153.45 | 1980 | 322.01 |
| 1966 | 83.26 | 1981 | 89.87 |
| 1967 | 163.63 | 1982 | 42.78 |
| 1968 | 72.20 | 1983 | 4.17 |
| 1969 | 195.82 | 1984 | 4.54 |
| 1970 | 608.43 | 1985 | 27.24 |
| 1971 | 195.63 | 1986 | 7.55 |
| 1972 | 81.05 | 1987 | 20.67 |
| 1973 | 745.98 | 1988 | 42.90 |
| 1974 | 354.25 | 1989 | 16.05 |
| 1975 | 819.93 | 1990 | 11.96 |
| 1976 | 293.77 | | |
| **Pacific sardine *Sardinops sagax*** | | | |
| 1962 | — | 1977 | — |
| 1963 | 0.77 | 1978 | — |
| 1964 | 0.90 | 1979 | — |
| 1965 | 0.04 | 1980 | — |
| 1966 | 0.02 | 1981 | 0.01 |
| 1967 | — | 1982 | 0.12 |
| 1968 | — | 1983 | 0.15 |
| 1969 | — | 1984 | 1.88 |
| 1970 | — | 1985 | 34.37 |
| 1971 | — | 1986 | 19.87 |
| 1972 | — | 1987 | 11.76 |
| 1973 | — | 1988 | 77.11 |
| 1974 | — | 1989 | 6.23 |
| 1975 | — | 1990 | 11.83 |
| 1976 | — | | |
| **Pacific bonito *Sarda chiliensis*** | | | |
| 1962 | 1.18 | 1977 | 0.14 |
| 1963 | 6.28 | 1978 | 4.35 |
| 1964 | 2.32 | 1979 | 0.31 |
| 1965 | 3.47 | 1980 | 0.33 |
| 1966 | 10.16 | 1981 | 1.73 |
| 1967 | 5.34 | 1982 | 0.38 |
| 1968 | 3.06 | 1983 | 0.96 |
| 1969 | 1.50 | 1984 | 8.17 |
| 1970 | 0.87 | 1985 | 3.22 |
| 1971 | 2.93 | 1986 | 0.22 |
| 1972 | 2.28 | 1987 | 1.55 |
| 1973 | 2.98 | 1988 | 1.55 |
| 1974 | 1.40 | 1989 | 0.98 |
| 1975 | 0.48 | 1990 | 0.76 |
| 1976 | 0.43 | | |
| **Pacific mackerel *Scomber japonicus*** | | | |
| 1962 | 2.74 | 1977 | 72.30 |
| 1963 | 6.62 | 1978 | 142.26 |
| 1964 | 1.06 | 1979 | 63.75 |
| 1965 | 0.41 | 1980 | 39.10 |
| 1966 | 0.23 | 1981 | 31.59 |
| 1967 | — | 1982 | 26.71 |
| 1968 | — | 1983 | 8.89 |
| **Pacific mackerel *Scomber japonicus* (continued)** | | | |
| 1969 | 0.03 | 1984 | 72.44 |
| 1970 | 0.83 | 1985 | 88.73 |
| 1971 | 0.13 | 1986 | 41.77 |
| 1972 | 0.03 | 1987 | 17.38 |
| 1973 | 0.18 | 1988 | 21.66 |
| 1974 | — | 1989 | 3.53 |
| 1975 | 0.02 | 1990 | 3.18 |
| 1976 | 0.47 | | |
| **Jack mackerel *Trachurus symmetricus*** | | | |
| 1962 | 5.04 | 1977 | 60.40 |
| 1963 | 13.73 | 1978 | 82.54 |
| 1964 | 11.56 | 1979 | 19.13 |
| 1965 | 9.97 | 1980 | 9.23 |
| 1966 | 2.70 | 1981 | 4.42 |
| 1967 | 6.61 | 1982 | 6.15 |
| 1968 | 11.41 | 1983 | 1.56 |
| 1969 | 3.55 | 1984 | 1.82 |
| 1970 | 1.87 | 1985 | 1.61 |
| 1971 | 5.91 | 1986 | 1.44 |
| 1972 | 6.27 | 1987 | 1.01 |
| 1973 | 0.21 | 1988 | 0.47 |
| 1974 | 1.88 | 1989 | 1.37 |
| 1975 | 5.69 | 1990 | 0.23 |
| 1976 | 3.89 | | |
| **Bluefin tuna *Thunnus thynnus*** | | | |
| 1962 | 4.40 | 1977 | 7.12 |
| 1963 | 6.81 | 1978 | 30.07 |
| 1964 | 6.81 | 1979 | 12.32 |
| 1965 | 0.90 | 1980 | 0.69 |
| 1966 | 9.46 | 1981 | 0.80 |
| 1967 | 3.42 | 1982 | 0.80 |
| 1968 | 6.03 | 1983 | 0.20 |
| 1969 | 0.39 | 1984 | 0.66 |
| 1970 | 0.02 | 1985 | 2.57 |
| 1971 | 0.42 | 1986 | 3.03 |
| 1972 | 2.75 | 1987 | 0.55 |
| 1973 | 16.45 | 1988 | 0.56 |
| 1974 | 17.28 | 1989 | 0.48 |
| 1975 | 2.54 | 1990 | 0.35 |
| 1976 | 13.20 | | |

### Indices of apparent abundance

Abundance index levels in tons/block area flight (T/BAF) were calculated for the total area by species for day plus night observations for the years 1962–90 (Table 4). From the total area index, the general trend of species abundance can be obtained. However, an index designed to better represent abundance change of each species is needed; therefore, a second set of abundance index values was calculated using only data from a core area of abundance as determined for each species by day or night, depending upon which period best represented the abundance of the species (Squire 1972). With the exception of data from one aerial spotter pilot (computer file 26), all data collected during 1962–90 was used in this analysis.

Data reflecting number of sightings and tonnage observed and its geographical distribution were used to define the geographical limits of the core area for each species. The core area for each species was determined to include all or portions of the following zones: northern anchovy, zones C,D,G,H; Pacific sardine, zones C,D,G,H; Pacific bonito, zones C,D,G,J; chub mackerel, zones C,D,G,H,I; jack mackerel, zones D,F,G,H,I; bluefin tuna, zones I,K,L,N,P (Fig. 1). For each species, the number of block areas in each zone comprising its core area and the total number of block areas in its core area are given in Table 5.

The core-area index is the mean of the T/BAF weighted to account for differences in size of core area within the zone to obtain a stratified mean (Cochran 1966). For each zone, the weight factor was the ratio of the total number of block areas having high species density in the zone to the total number of block areas

**Table 5**

Areas of high density determining core-area abundance, by species.

| Core area determined for | | |
|---|---|---|
| **Northern anchovy**<br>***Engraulis mordax*** | Zone G = | 10 block areas |
| | D = | 11 " " |
| | C = | 10 " " |
| | H = | 6 " " |
| | | 37 block areas comprising the anchovy core area |
| **Pacific sardine**<br>***Sardinops sagax*** | Zone C = | 6 block areas |
| | D = | 5 " " |
| | G = | 5 " " |
| | H = | 4 " " |
| | | 20 block areas comprising the Pacific bonito core area |
| **Pacific bonito**<br>***Sarda chiliensis*** | Zone C = | 6 block areas |
| | D = | 8 " " |
| | G = | 8 " " |
| | J = | 7 " " |
| | | 29 block areas comprising the Pacific bonito area |
| **Chub mackerel**<br>***Scomber japonicus*** | Zone G = | 6 block areas |
| | H = | 3 " " |
| | I = | 3 " " |
| | D = | 5 " " |
| | C = | 4 |
| | | 21 block areas comprising the Pacific mackerel core area |
| **Jack mackerel**<br>***Trachurus symmetricus*** | Zone D = | 8 block areas |
| | G = | 7 " " |
| | H = | 3 " " |
| | I = | 3 " " |
| | F = | 4 " " |
| | | 25 block areas comprising the jack mackerel core area |
| **Bluefin tuna**<br>***Thunnus thynnus*** | Zone I = | 20 block areas |
| | L = | 20 " " |
| | K = | 15 " " |
| | N = | 18 " " |
| | P = | 8 " " |
| | | 81 block areas comprising the bluefin tuna core area |

with high density comprising the entire core area. Core-area abundance (weighted T/BAF) is

$$\sum w_i\ (t/BAF)_i,$$

where $W_i$ – weight for zone i = a/b
a = blocks in core area from zone i
b = total blocks in core area, all zones
$(T/BAF)_i$ = T/BAF for zone i.

## Abundance trends by species

Core-area index values in Figs. 2–7 are presented as a weighted mean index and as a running average of three to better illustrate trends in abundance. Core-area abundance index values are given in Table 6.

### Table 6

Core-area index values in T/BAF, day or night in T/BAF. Dash indicates an abundance level <0.01 T/BAF.

| Year | Core area | Year | Core area |
|---|---|---|---|
| **Northern anchovy *Engraulis mordax*** | | | |
| 1962 | 0.09 | 1977 | 858.73 |
| 1963 | 250.98 | 1978 | 263.89 |
| 1964 | 160.55 | 1979 | 624.80 |
| 1965 | 253.85 | 1980 | 578.68 |
| 1966 | 116.92 | 1981 | 236.71 |
| 1967 | 225.70 | 1982 | 67.86 |
| 1968 | 173.41 | 1983 | 7.72 |
| 1969 | 309.84 | 1984 | 6.76 |
| 1970 | 629.03 | 1985 | 47.88 |
| 1971 | 362.59 | 1986 | 13.39 |
| 1972 | 54.55 | 1987 | 33.28 |
| 1973 | 1143.55 | 1988 | 69.20 |
| 1974 | 494.29 | 1989 | 7.24 |
| 1975 | 1010.70 | 1990 | 31.45 |
| 1976 | 456.10 | | |
| **Pacific sardine *Sardinops sagax*** | | | |
| 1962 | — | 1977 | — |
| 1963 | 1.38 | 1978 | — |
| 1964 | 1.31 | 1979 | — |
| 1965 | 0.02 | 1980 | — |
| 1966 | 0.03 | 1981 | — |
| 1967 | 225.70 | 1982 | 0.24 |
| 1968 | 0.01 | 1983 | 0.33 |
| 1969 | — | 1984 | 2.77 |
| 1970 | — | 1985 | 97.36 |
| 1971 | — | 1986 | 32.35 |
| 1972 | — | 1987 | 20.12 |
| 1973 | — | 1988 | 145.75 |
| 1974 | — | 1989 | 34.84 |
| 1975 | — | 1990 | 39.03 |
| 1976 | — | | |
| **Pacific bonito *Sarda chiliensis*** | | | |
| 1962 | 2.20 | 1977 | 0.23 |
| 1963 | 2.29 | 1978 | 0.96 |
| **Pacific bonito *Sarda chiliensis* (continued)** | | | |
| 1964 | 3.39 | 1979 | 0.38 |
| 1965 | 5.88 | 1980 | 0.38 |
| 1966 | 14.84 | 1981 | 1.78 |
| 1967 | 7.20 | 1982 | 0.56 |
| 1968 | 3.35 | 1983 | 1.31 |
| 1969 | 1.58 | 1984 | 9.93 |
| 1970 | — | 1985 | 3.98 |
| 1971 | 3.47 | 1986 | 0.30 |
| 1972 | 2.83 | 1987 | 1.05 |
| 1973 | 3.34 | 1988 | 2.42 |
| 1974 | 1.76 | 1989 | 1.23 |
| 1975 | 0.74 | 1990 | 1.15 |
| 1976 | 0.59 | | |
| **Chub mackerel *Scomber japonicus*** | | | |
| 1962 | 4.04 | 1977 | 104.80 |
| 1963 | 3.36 | 1978 | 198.72 |
| 1964 | 1.63 | 1979 | 85.27 |
| 1965 | 0.80 | 1980 | 58.78 |
| 1966 | 0.51 | 1981 | 41.74 |
| 1967 | 0.01 | 1982 | 29.24 |
| 1968 | 0.01 | 1983 | 19.00 |
| 1969 | 0.07 | 1984 | 59.91 |
| 1970 | 2.95 | 1985 | 148.18 |
| 1971 | 0.33 | 1986 | 85.48 |
| 1972 | 0.10 | 1987 | 36.06 |
| 1973 | 0.48 | 1988 | 43.55 |
| 1974 | — | 1989 | 7.83 |
| 1975 | — | 1990 | 3.19 |
| 1976 | 0.05 | | |
| **Jack mackerel *Trachurus symmetricus*** | | | |
| 1962 | 5.28 | 1977 | 91.41 |
| 1963 | 23.10 | 1978 | 74.90 |
| 1964 | 14.69 | 1979 | 20.13 |
| 1965 | 14.58 | 1980 | 12.25 |
| 1966 | 4.49 | 1981 | 7.77 |
| 1967 | 15.26 | 1982 | 10.14 |
| 1968 | 24.21 | 1983 | 2.20 |
| 1969 | 5.68 | 1984 | 7.47 |
| 1970 | 2.91 | 1985 | 6.23 |
| 1971 | 12.55 | 1986 | 2.63 |
| 1972 | 11.65 | 1987 | 1.69 |
| 1973 | 0.39 | 1988 | 1.03 |
| 1974 | 3.41 | 1989 | 2.86 |
| 1975 | 13.17 | 1990 | 0.81 |
| 1976 | 11.59 | | |
| **Bluefin tuna *Thunnus thynnus*** | | | |
| 1962 | 6.57 | 1977 | 8.71 |
| 1963 | 6.97 | 1978 | 34.52 |
| 1964 | 6.97 | 1979 | 12.87 |
| 1965 | 1.28 | 1980 | 0.89 |
| 1966 | 13.03 | 1981 | 0.95 |
| 1967 | 4.51 | 1982 | 1.37 |
| 1968 | 9.45 | 1983 | 0.05 |
| 1969 | 0.59 | 1984 | 0.62 |
| 1970 | — | 1985 | 2.32 |
| 1971 | 0.87 | 1986 | 1.98 |
| 1972 | 6.94 | 1987 | 0.77 |
| 1973 | 17.38 | 1988 | 1.23 |
| 1974 | 18.32 | 1989 | 1.02 |
| 1975 | 2.60 | 1990 | 0.73 |
| 1976 | 13.73 | | |

**Northern anchovy (Fig. 2)** The core area index (night index) was near 180 T/BAF in the mid- to late-1960s. The index increased in the early 1970s, and during 1972–80 remained in the range of 450–700 T/BAF. The index began to decline in 1980 and reached a low level of abundance by 1983 (<50 T/BAF), a level considerably below that observed in the mid-1960s.

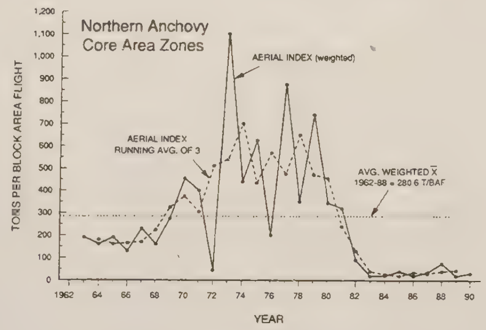

**Figure 2**

Abundance index levels in T/BAF for northern anchovy *Engraulis mordax* core area, night index, weighted $\bar{x}$, and running average (×3).

**Pacific sardine (Fig. 3)** The Pacific sardine resource was in a state of decline at the time the aerial spotter program was started. Average tonnage calculated for the 1963–66 period for the core-area index was 1.03 T/BAF. Very low abundance indices were recorded from 1967 until the early 1980s with some years reporting zero sightings of sardine schools. The core-area running mean index (night index) increased to 60 T/BAF by 1988.

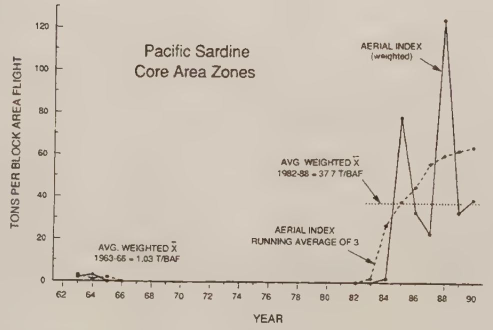

**Figure 3**

Abundance index levels in T/BAF for Pacific sardine *Sardinops sagax* core area, night index, weighted $\bar{x}$, and running average (×3).

**Pacific bonito (Fig. 4)** Abundance levels for Pacific bonito show considerable fluctuation. Bonito were rarely taken off southern California prior to the strong El Niño of 1957–58 (Radovich 1960). They were common in southern California waters after this event and were intensively fished starting in about 1963. The increase in fishing effort redirected to this species was the result of decreased abundance of Pacific sardine and chub mackerel.

The core-area index value (day index) reached a high in 1966 of 10.5 T/BAF. This is the highest index value recorded for bonito during 1962–90. The index then declined, increased slightly in 1972 to 3.2 T/BAF, and substantially increased in 1984 to 5.5 T/BAF.

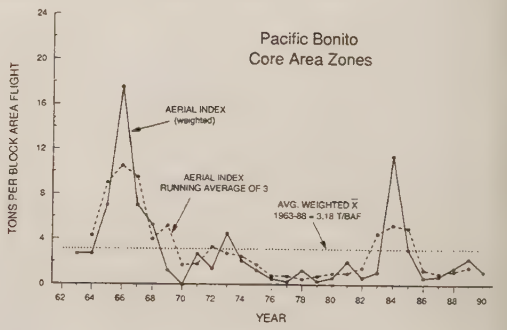

**Figure 4**

Abundance index levels in T/BAF for Pacific bonito *Sarda chiliensis* core area, day index, weighted $\bar{x}$, and running average (×3).

**Chub mackerel (Fig. 5)** Declining abundance levels noted in the early to mid-1960s matched the collapse of the fishery, with extremely low index levels (>5 T/BAF) noted for the core-area index (night index) in 1967–75. After 1976, the abundance index rose rapidly to a peak of 170 T/BAF in 1978, then declined to a range of 15–55 T/BAF in 1981–89.

**Jack mackerel (Fig. 6)** Abundance was high during the mid 1970s. The core-area index (night index) increased to 234 T/BAF in 1976 and declined to <10 T/BAF after 1979.

**Bluefin tuna (Fig. 7)** For the core area, there were three peaks in the index (day index) of abundance: 1967, 1973, and 1978. The index for recent years is well below the 1963–88 average of 10.8 T/BAF.

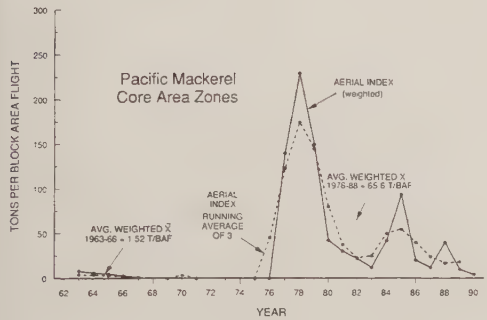

**Figure 5**
Abundance index levels in T/BAF for chub mackerel *Scomber japonicus* core area, night index, weighted $\bar{x}$, and running average (×3).

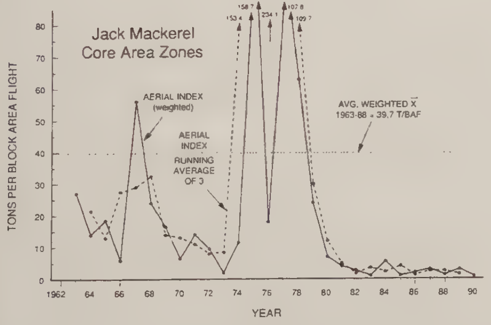

**Figure 6**
Abundance index levels in T/BAF for jack mackerel *Trachurus symmetricus* core area, night index, weighted $\bar{x}$, and running average (×3).

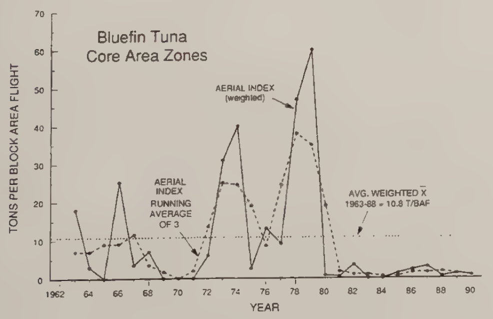

**Figure 7**
Abundance index levels in T/BAF for bluefish tuna *Thunnus thynnus* core area, night index, weighted $\bar{x}$, and running average (×3).

## Interaction between species

To compare periods of high and low abundance of the six species, the logarithm of the moving weighted averages of core-area abundance indices (day or night, dependent upon which time the species was observed more frequently and in greater quantity) were plotted (Fig. 8). The dominant feature of Fig. 8 is the abundance index for the northern anchovy. High index levels of 200–500 T/BAF were recorded during 1962–82, a 21 yr period. The index declined sharply in 1983 and 1984, increasing since. The northern anchovy is the more stable species in terms of less annual percentage change in abundance than any of the other five species. During 1966 and 1967, jack mackerel, bluefin tuna, and Pacific bonito were at higher levels of abundance than those observed in the early 1970s. The Pacific sardine and chub mackerel resources were low in abundance by 1965, and declined to extremely low levels by 1970. The northern anchovy, jack mackerel, chub mackerel, and bluefin tuna increased in abundance in 1974–79. Exceptions were the Pacific bonito and sardine.

The very strong El Niño condition of 1982–83 (Quinn et al. 1987) had a significant effect on the distribution of coastal pelagic species (Fluharty 1984, Squire 1987). This period saw declines in abundance for all species, except Pacific bonito and chub mackerel. These two species showed significant declines in 1986–87. A rapid increase in Pacific sardine abundance was evident in 1984, immediately following the El Niño event and continuing into the late 1980s.

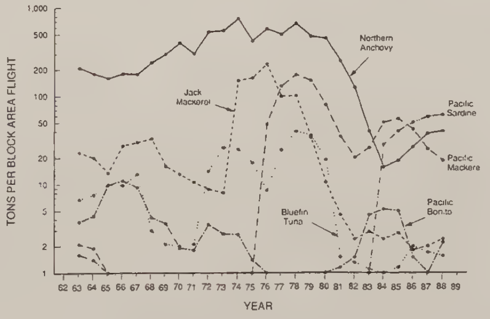

**Figure 8**
Comparison of core-area fluctuations in apparent abundance index levels for northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, chub mackerel *Scomber japonicus*, Pacific bonito *Sarda chiliensis*, jack mackerel *Trachurus symmetricus*, and bluefin tuna *Thunnus thynnus*. Data plotted on a semi-logarithmic scale, in weighted $\bar{x}$, T/BAF, by moving average (×3).

From inspection of core-area fluctuations (Fig. 8), it is difficult to draw any conclusions regarding interaction among most of the species included in this study. The annual abundance values that appear to be more closely related are those of the northern anchovy and bluefin tuna which were significantly correlated ($y=0.76$, $P<0.1$).

## Pilot estimation of tonnage

Differences between pilots' ability to estimate school or group size are difficult to evaluate using the type of data recorded in flight logs. Computer recording of flight track and species tonnage observed did not include details of what portion of the block was searched, or where the species were sighted. Aerial spotters entering the block area (an 8×10 nm area) may have observed fish schools of the same species in two geographically different locations. Only the sum of the school sizes was coded.

The time of observation is probably the most critical factor in comparisons of pilot sightings because near-surface fish abundance may be highly variable over a short period of time. Therefore, unless pilots are searching the same area at the same time, different levels of abundance are likely to be observed.

Williams (1981) in surveys of pelagic fish resources off southeast Australia indicated that the professional fish spotters were extremely accurate in tonnage estimates of individual schools. In tests conducted by NMFS and CDF&G to determine northern anchovy school size using acoustic gear, a purse seiner and aerial spotter were used. The aerial spotter had a more accurate estimate of school tonnage than obtained from acoustic gear (P. Mardesich, Flying Fishermen, Inc., pers. commun. 1978).

MacCall (1975), using the NMFS computer database, investigated variation in anchovy abundance estimates (comparison of data collected during the same 10d period in 1973 and 1975) and found considerable differences among spotters. The differences were consistent for individual pilots for day and night observations. Variability in reported tonnage was large, but it could be reduced by long-term averaging. MacCall (1975) further suggested that corrections for pilots estimating efficiency be incorporated in calculations of the abundance index to avoid biasing the result toward the spotter with the highest tonnage. The accuracy of fish-spotter estimates of tonnage was approached statistically by Lo et al. (In press) using a delta-lognormal model. All aerial spotter data were used in this analysis. However, until spotter-pilot estimating efficiency is measured in field experiments, correction factors are unknown. It is possible that these differences between spotters may be due more to differences in numbers of schools seen than to differences in size estimates.

## Comparison of aerial index to other abundance indices

The problem of variability among spotter pilots complicates comparisons; however, pilots are paid relative to the amount of tonnage caught. Therefore, the aerial spotter needs to have a reasonable estimate of school size to compare with the amount of fish caught by the seiner. The aerial spotter is continually obtaining "ground truth" from the purse-seine vessel relative to species composition and size of the school caught.

Since the decline of the Pacific sardine resource in 1984, considerable effort has been expended on surveys, using various techniques to collect apparent abundance data that could be modeled to produce an estimate of biomass. Acoustic, egg and larva, and aerial-spotter surveys have been conducted. Each survey measures a different component of the population and, therefore, comparisons of abundance estimates from different methods and models must be viewed with caution.

The aerial-spotter program measures apparent abundance of adults and subadults of epi-pelagic schooling fishes, and assumes that most adults in the population are available to the spotters at some time during the year. The aerial index is a direct calculation (T/BAF). It is a non-random type survey, but is not time-restricted.

The operational procedures used by aerial spotters affect the results. Although they do work closely with the fleet in locating and sometimes directing the setting of the purse seine, much of their time is spent searching large areas of the ocean for fishable resources. Many times, the aerial spotter will conduct flight operations in a general survey mode for the fleet, but does not work directly with the fleet. Even though aerial monitoring is conducted throughout the year, most observation effort is in the summer and early fall (49% of BAF during July, August, and September) when concentrations of commercial species are more common in the nearshore areas.

Quantitative apparent-abundance data derived from field surveys (egg and larvae, and acoustic) are statistically treated under various biological assumptions to ultimately obtain an estimate of biomass or tonnage: spawning biomass and total biomass in the case of egg and larva surveys (Lo 1985), and schooled biomass in the case of acoustic surveys (Mais 1974). Although some biomass estimates have been made for other species, such as the chub mackerel and Pacific sardine, most biomass studies and modeling for the California region have involved the northern anchovy (Methot 1989).

Over the past 35 yr, studies by fishery biologists have produced a wide range of population estimates for a number of the pelagic species, in particular, the northern anchovy, Pacific sardine, and chub mackerel. The following describes the results of these and others in relation to aerial abundance indices.

**Northern anchovy** A review of the many abundance estimates for the northern anchovy over the years 1940–66 was given by Messersmith et al. (1969). For the early years of the aerial program, MacCall et al. (1974) compared anchovy biomass estimates from egg and larva surveys with the night aerial index, resulting in a correlation of +0.30 (1962–69). They also compared the aerial night index with the acoustic estimate (1966–72) producing a negative correlation ($r=-0.47$).

In a review of egg production of the northern anchovy central stock, Lo (1985) presented a correlation between various indices of anchovy spawning biomass. The biomass index from the aerial surveys had a high correlation ($r=0.818$) with egg production, and there was a similar correlation ($r=0.807$) between biomass egg production and acoustic surveys.

Correlation plots of normalized data (standard deviates; Snedecor 1959) were used to compare northern anchovy abundance data presented by Lo (1988) with aerial index values. The aerial index (day plus night) for the core area was compared with Lo's (1988) estimate of spawner biomass, determined from a combination of various estimates from the egg production method and the results of the 1969–85 sonar or acoustic surveys (Lo 1988), giving a correlation of $r=0.61$, df=14, $P<0.05\%$. The aerial index was also compared with the estimate of schooled biomass based on results of acoustic surveys presented by Lo (1988), giving a correlation of $r=0.51$, df=13, $P<0.05\%$.

MacCall & Prager (1988) presented anchovy larval-abundance indices for 1963–85. These indices, which are a measure of spawning population, were compared with the core-area aerial index for the same set of years. There was statistically significant correlation between the two indices (aerial/larva) ($r=0.82$, df=13, $P<0.1$).

**Pacific sardine** MacCall & Prager (1988) also reviewed the historical trend of sardine larval abundance, 1951–85. A comparison was made between their arithmetic scale of larval abundance (standard index) and the aerial index during the period 1963–85. Indications of a resurgence of the Pacific sardine resource began in 1978, and for the 1963–85 period MacCall & Prager's (1988) estimate of larval abundance correlates well with the aerial index ($r=0.98$, df=8, $P<0.01$).

**Pacific bonito** Pacific bonito, a species whose seasonal abundance off California is more closely associated with environmental conditions (El Niño effects) than the other species (Squire 1987), has not been subjected to detailed assessment. MacCall et al. (1974) used recreational partyboat CPUE data in yearly time-lag periods and compared this with the aerial index. The recreational partyboat fleet generally fishes nearshore and catches younger fish than the offshore commercial purse-seine fleet. The highest correlation ($r=0.69$) between the recreational fleet CPUE and the aerial index was for a 3 yr lag period (aerial index lags the recreational CPUE). No other independent estimates of Pacific bonito biomass are available for comparison.

**Chub mackerel** Assessment of the chub mackerel resource has used both standard population-dynamics techniques and methods that utilize egg and larva surveys. For comparison of changes in population over time, Squire (1983) plotted the trend of the aerial index against the spawning biomass index and the larva index of Smith & Richardson (1977). The limited data (1963–67) precluded any long-term comparison; however, all three indices showed a similar decrease. The aerial index was significantly correlated ($P<0.05$) with both spawning biomass ($r=0.99$) and the larva index ($r=0.94$).

The chub mackerel biomass declined to very low levels in the mid-1960s and remained very low until the mid-1970s. A sharp increase in biomass was noted starting in 1976. MacCall & Prager (1988) presented data on chub mackerel larval abundance through 1985. A correlation of the aerial index (core area) with the larva index for 1963–81 was statistically insignificant ($r=0.205$). A comparison made between the aerial index (core area) and estimated biomass of MacCall et al. (1985) for 1963–84 gave what would appear to be a good fit for the early years, but comparison of later years' estimates was not significant ($r=0.26$).

**Jack mackerel** Various indices of abundance for jack mackerel, including the aerial index, show that the resource tends to be highly variable in apparent abundance. Egg and larva surveys have shown the stock to be extremely widespread. Based on tagging data, Knaggs (1973) estimated between 700,000 and 1,500,000 t were available to the fishery in 1973. MacCall et al. (1974) stated that these estimates are in agreement with trends in aerial survey index (Squire

1972). MacCall & Prager (1988) presented graphics on a time-series of abundance indices for jack mackerel larva off southern California. They noted that the index did not correspond well with other larval indices that included samples from central California. An examination of the MacCall & Prager (1988) larva index vs. the aerial index indicated a poor correlation ($r$=0.16, not significant), particularly for the years 1977–78, a period of marked increase in jack mackerel abundance off southern California.

**Bluefin tuna** No biomass estimates are available for bluefin tuna in the northeast Pacific, which is part of a Pacific-wide resource. Young year-classes (1–3 yr) are common in the northeast Pacific with some catches of fish up to 6 yr of age (Bayliff 1980). CPUE estimates presented by Calkins (1982) of catch/boat-day (C/BD) for the U.S. purse-seine fishery operating off California and Baja California, Mexico for the years 1963–80 in the area north of 29° N lat. were compared with the aerial core-area mean index. Although both indices (C/BD and T/BAF) show a decline prior to 1980, the correlation was not significant ($r$=0.033). Calkins (1982) stated that "total catch may be the best indicator of bluefin abundance." Total catch (north of 29° N lat.) as given by Calkins (1982) was compared with the core-area index, and the correlation was again not significant ($r$=0.147).

## Summary and conclusions

The aerial monitoring program has produced information on the trend of apparent abundance for six species of pelagic near-surface schooling species. The program in operation since 1962 utilizes information provided by commercial aerial fish spotters. Spotter pilots operate under strong incentive to estimate tonnage accurately, since their compensation is based on actual tonnage caught. The cost of the program is a small fraction of the cost of other field assessment methods currently used to develop apparent abundance data, such as egg and larva surveys and acoustic surveys.

Data are presented in a relatively simple and understandable index format of tons observed/block area searched (T/BAF). Annual indices (T/BAF) of apparent abundance are calculated for the major species of importance to the commercial purse-seine fleet operating off southern California and northwestern Baja California, Mexico.

All species have shown a fluctuating pattern of apparent abundance over the 29 yr survey period (1962–90). The northern anchovy is the dominant species observed, accounting for 89.7% of all tonnage observed; chub mackerel is second with 6.1%; followed by jack mackerel with 2.1%, and Pacific sardine, Pacific bonito, and bluefin tuna with 2.1%.

From inspection of abundance data, peak periods of higher abundance for four of the six species (chub mackerel, jack mackerel, northern anchovy, and bluefin tuna) occurred in 1977–79. Analysis indicated that species more closely related in abundance over time are the northern anchovy and bluefin tuna, both being at higher levels of abundance during 1972–80. A regression was calculated for 1963–88, giving a significant correlation ($r$=0.76, $P$<0.1).

A number of comparisons were made between estimates of biomass (spawning or total biomass) and the aerial abundance indices for the northern anchovy, Pacific sardine, and chub mackerel, and the apparent abundance of bluefin tuna based on CPUE data. There is a significant correlation with the aerial index, the anchovy total biomass estimate, and the historical egg-production index. Also, there was a slightly less but significant correlation with the acoustic survey estimates. The more significant correlations were found in comparing the aerial index with the northern anchovy larva index and the Pacific sardine larva index. For the chub mackerel, a species recognized as having a highly fluctuating record of abundance, the correlations during the early years (1963–66) were very good (aerial index vs. larva index and spawning biomass index); in later years, correlations between the larva index and the estimates of total biomass and the aerial index were not significant. There is a lack of good data relative to the abundance for other species of interest (Pacific bonito, jack mackerel, bluefin tuna) although some comparisons with the aerial data have been made for Pacific bonito, giving a reasonable correlation using a 3 yr lag period. Bluefin tuna C/BD (catch/boat-day) and total catch for the northwest Mexico–southern California fishery were compared with the aerial core index and gave no significant correlation.

Trends of aerial indices indicate that the pelagic resources studied can be described in a state of chaotic fluctuations (Jensen 1987) relative to apparent abundance. The fluctuating record indicates that even short-term predictions of abundance appear not to be feasible. Management must rely on near real-time estimates based on a measurement of a small fraction of the resource, and what is important is the development and use of more than one method or approach in evaluating population status. None of the survey results appear in complete agreement; however, utilizing several approaches to provide "triangles of agreement" (from a method used in navigation) can provide a consensus for management action.

## Acknowledgments

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# IMPLICATIONS OF NON-LINEAR DENSITY DEPENDENCE

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## ABSTRACT

Ranges of the ratio of maximum net productivity level (MNPL) to carrying capacity (*K*) are explored in general models for pinnipeds and odontocetes. MNPL/*K* is used in management of marine mammals but no empirical evidence exists to limit the range of values expected. Density dependent changes in age-specific birth and death rates have been used to infer MNPL/*K*. Non-linearities in these rates do not translate directly to population growth curves. The simple models demonstrate: (1) density dependence is likely to involve more than a single parameter (such as birth rate), (2) MNPL/*K* can be greatly reduced from that inferred from one strongly non-linear parameter when changes in other parameters are linear, (3) ranges of MNPL/*K* depend on biological limits on ranges of fecundity and survival rates, and (4) the magnitude and sign of bias incurred by inferring MNPL/*K* from functional forms of single parameters cannot be determined. Given current empirical evidence the range of MNPL/*K* for marine mammals as a group is large. Although MNPL/*K* should not be inferred from single parameter non-linearities, distributions of MNPL/*K* values can be generated through models which account for single species ranges for birth and death rates and maximum population growth rate.

Key words: demography, density dependence, logistic, marine mammal, non-linear dynamics, odontocete, pinniped, population dynamics.

Density dependent population dynamic models are used routinely in the management of marine mammals (Gerrodette and DeMaster 1990). Populations are typically managed relative to the population level where the maximum sustainable yield is realized (Donovan 1989) or the population level where net productivity is maximized. Maximum net productivity level (MNPL) is defined as (Gehringer 1976), ". . . the greatest net annual increment in population numbers or biomass resulting from additions to the population due to reproduction and/or growth less losses due to natural mortality." Empirical data concerning population growth rates at different population sizes for marine mammals are limited. Population growth is usually represented by deterministic models which describe the future state of a population given the current state. The state is given in terms of numbers of individuals. These population growth models, such as the logistic or various modified logistic models, consider all individuals to be equal with respect to future prospects of birth and death, that is, age structure is not explicitly used in the models.

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Although the data for the relationship between population growth and population size are sparse for marine mammals, data on some age-specific birth and death rates are available for a few species. Based on these data, MNPL has been inferred to be above 0.5$K$ (Fowler *et al.* 1980, Fowler 1987). From a model using an evolutionary argument, Fowler *et al.* (1980) state: "We would expect a whale population with a maximum specific productivity of 0.04 to show its greatest productivity levels between 88 and 92 percent of its equilibrium level." However, using the relationship from Fowler (1987), with a generation time of 20 yr and a maximum specific productivity of 0.04, would result in MNPL/$K$ of 0.67. The purpose of this paper will be to explore the range of MNPL/$K$ values possible for different combinations of density dependent age-specific changes in birth and death rates. Special attention will be given to biases which could result from inferring MNPL/$K$ from density dependent changes in a single age-specific parameter. Two simple models will be used to explore whether what is known about non-linearities in age-specific birth and death rates justifies acceptance of any particular range of MNPL/$K$ values. The first model is a generalized pinniped model which represents the marine mammal life history with the fastest population growth rate. At the other end of the spectrum, a generalized odontocete model is used to represent life history strategies with slow growth rates.

*Empirical evidence*—General reviews of empirical evidence for density dependence in large mammals, with separate sections on marine mammals, are presented in Fowler (1987) and Fowler *et al.* (1980). The intent of this paper is not to focus on any particular species but rather to present what general forms may pertain to specific demographic parameters. Fowler (1984) reviews density dependence in marine mammals and finds evidence of regulation for fecundity in nine species, age of first reproduction (AFR) in ten species, juvenile survival in five species and adult survival in one species. These frequencies may reflect ease of gathering data. For example, although adult survival may be density dependent, estimation is difficult and power to detect a change would be low for the amount of change required to affect population growth rates. The lack of empirical evidence makes the form of density dependence for adult survival purely speculative.

A recent reanalysis (de la Mare 1992) of some data reviewed by Fowler *et al.* (1980) shows the inability to draw general conclusions about the shape of recruitment functions. The following statements can be made based on empirical data (Fowler *et al.* 1980, de la Mare 1992): (1) marine mammals show density dependent responses, (2) for species for which data are available over a range of population sizes, density dependent responses are not abrupt (knife-edge),

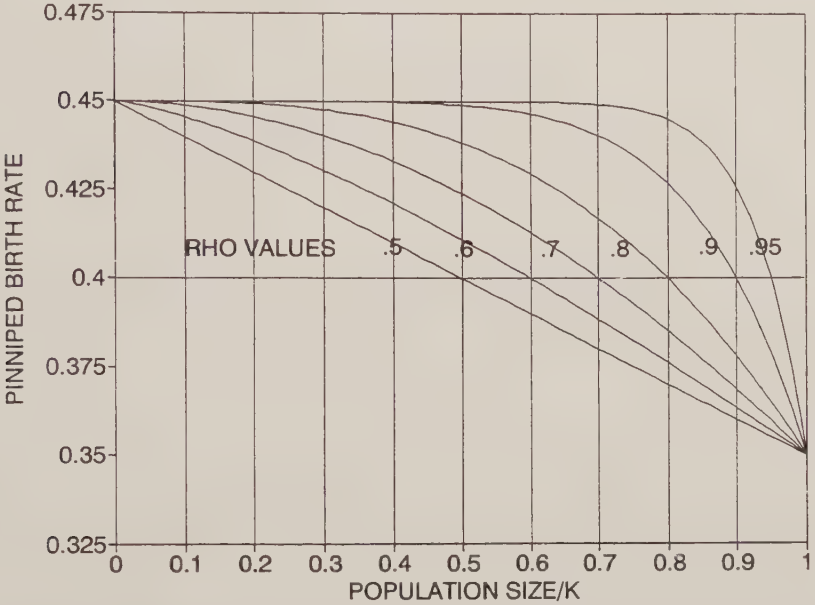

*Figure 1.* Curves for the Allen equation (Equation 3) for different $\rho$-values for birth rates for pinnipeds. The horizontal line indicates the point of 50% change in the parameter range. Note the intersections of the functions for different $\rho$-values with this line.

and (3) density dependent responses have not been shown to be concave (higher rates of change at low density), though the power is low. In this paper, a concave curve is one in which the value for any point between two endpoints is less than the value which would be a linear interpolation. Given the endpoints (0, 1) and (1, 0), a linear relation would yield a $y$-value of 0.5 when $x = 0.5$. A curve passing through any $y$-value $<0.5$ at $x = 0.5$ would be concave. None of the curves in Figure 1 are concave. A theoretical argument has been given by de la Mare and Cooke (1992) that concave responses are possible by allowing spatial variation in the environment. For the purposes of this paper, responses are limited to range from linear to strongly convex (most density dependent response at levels very close to $K$). Given current quantities and qualities of empirical data, it is not possible to further limit functional forms of age-specific density dependent responses for marine mammals as a group.

*Theoretical arguments*—Although MNPL is defined in population terms, empirical data exist primarily for age-specific demographic rates. We now consider how each approach is represented theoretically. Density dependent population growth is commonly represented by the generalized logistic equation (Pella and Tomlinson 1969, Gilpin *et al.* 1976) (altered below for discrete growth).

$$N_{t+1} = N_t + (\lambda_{\max} - 1)N_t\left[1 - \left(\frac{N_t}{K}\right)^{\theta}\right] \tag{1}$$

where $N$ = population size, $t$ = time, $K$ = carrying capacity, $\lambda_{\max}$ = maximum discrete rate of population growth, and $\theta$ = shape parameter. Goodman (1980) showed distortion in the population growth curve caused by age structure: a linear change in birth rate caused the population growth curve to be convex. The convex shape of density dependent birth and survival functions argues generally for a maximum growth rate which is greater than $K/2$ ($\theta > 1$).

The $\theta$-logistic equation does not include age-specific mortality or fecundity, but rather uses a single parameter, discrete population growth rate ($\lambda$, where $\lambda_{Nt} = N_{t+1}/N_t$), to predict the next population size given the current population size. For any given set of age-specific birth and death parameters there is a unique population growth rate which satisfies the equation:

$$1 = \sum_{x=AFR}^{\omega} l_x m_x \lambda^{-x} \tag{2}$$

where $x$ = age, $AFR$ = age of first reproduction, $\omega$ = oldest age, $l$ = survivorship, $m$ = fecundity, and $\lambda$ = discrete rate of growth. Population growth is sensitive to different parameters in varying strengths. For example, equal proportional changes (called elasticity, Caswell 1989) in adult and juvenile survival rates will result in different changes to $\lambda$. For long-lived animals which have high adult survival rates and typically relatively low maximum population growth rates, $\lambda$ is most sensitive to changes in adult survival rate (Goodman 1981). Relatively large changes in birth and juvenile survival rates result in rather small changes in $\lambda$. For example, consider a case where the survival rate for the first year is 0.50 and is 0.95 thereafter. Let $AFR = 1$, $\omega = 20$, and $m = 0.5$ giving $\lambda = 1.051$. A 10% reduction in adult survival, juvenile survival, and birth rate results in $\lambda$ values of 0.972, 1.026, and 1.038 or changes of $-7.5\%$, $-2.4\%$, and $-1.2\%$ respectively. For this reason it is difficult to intuit how non-linear changes in birth or juvenile survival rates will affect $\lambda$ and the MNPL. Therefore, simple models will be used to investigate the translation of density dependent changes in birth and death rates into population growth rates.

## METHODS

*Introduction to the life history models*—The translation of several age-specific density dependent functions into a single population growth function is best illustrated with simplified population models. The following parameters characterize the demography: mean fecundity ($m$), annual adult survival rate ($p_a$), annual juvenile survival rate ($p_j$—from age zero to one), $AFR$, oldest age ($\omega$) and maximum discrete rate of growth ($\lambda_{\max}$). We chose parameter values based loosely on the life history of fur seals (*Callorhinus ursinus*) for the pinniped model (Ragen 1990), and the bottlenose dolphin (*Tursiops truncatus*) for the odontocete model (Scott *et al.* 1990, Wells and Scott 1990). Default values for each parameter were selected to give the growth rate expected at $K/2$ within known ranges for pinnipeds (Ragen 1990) and odontocetes (Scott *et al.* 1990,

*Table 1.* Default parameters to yield λ at K/2 assuming a linear decrease in per capita growth.

| Model | $\lambda(N = K/2)$ | $m$ | $AFR$ | $p_j$ | $p_a$ | $\omega$ |
|---|---|---|---|---|---|---|
| Pinniped | 1.05 | 0.40 | 5 | 0.423 | 0.960 | 20 |
| Odontocete | 1.02 | 0.12 | 10 | 0.593 | 0.980 | 50 |

Brault and Caswell 1993) (Table 1). Density dependent population growth was achieved by adjusting one or more of the above parameters.

*Changes in single parameters*—We begin examining the effect of changes in age-specific parameters on population growth rate by changing only a single parameter. The required single parameter changes needed to obtain growth rates from $\lambda = \lambda_{\max}$ to $\lambda = 1$ could then be solved given equation 1. Change between the minimum and maximum parameter values was governed by:

$$X_N = X_{N=K} + (X_{N=0} - X_{N=K})\left[1 - \left(\frac{N}{K}\right)^z\right] \tag{3}$$

where $N$ = population size, $K$ = carrying capacity ($\lambda = 1$), $X_{N=0}$ = the value of the parameter when $N = 0$, $X_{N=K}$ = the value of the parameter at $K$, and $z$ = shaping parameter. Because $z$-values are difficult to interpret, we have used a different scale. Let $\rho$ be the $N/K$ value reached when the $z$-value has changed half its range. Equation 3 can be rearranged to solve for $z$ given the desired $\rho$-value.

$$z = \frac{\ln(0.5)}{\ln(\rho)} \tag{4}$$

Using Equation 4, we find that if we want a given parameter to have changed 50% of its range when $N/K = 0.9$ then $z = 6.58$. We investigated $\rho$-values between 0.50 ($z = 1$) and 0.95 ($z = 13.5$). The knife-edge limitation is therefore defined as $\rho = 0.95$, when the parameter has changed 50% of its range in 0.95 ($N/K$). Equation 3 (Allen 1976) is shown for different $\rho$-values in Figure 1 for birth rate for pinnipeds.

*Changes in multiple parameters*—In order to reduce the number of permutations of multiple parameters, changes were allowed which met two criteria: (1) parameter values must be biologically reasonable, and (2) changes in $z$ must

*Table 2.* Minimum and maximum values allowed to maintain biological realism. Birth rate parameters assume a sex ratio of 0.5 and a maximum pregnancy rate of 90%. For the odontocete model calving interval is three years when $N = 0$ and five years when $N = K$.

| Model | $\lambda$ $X_{N=0}$ | $AFR$ $X_{N=0}$ | $AFR$ $X_{N=K}$ | $m$ $X_{N=0}$ | $m$ $X_{N=K}$ | $p_j$ $X_{N=0}$ | $p_j$ $X_{N=K}$ |
|---|---|---|---|---|---|---|---|
| Pinniped | 1.10 | 4 | 6 | 0.45 | 0.35 | 0.67 | 0.24 |
| Odontocete | 1.04 | 8 | 12 | 0.15 | 0.09 | 0.66 | 0.51 |

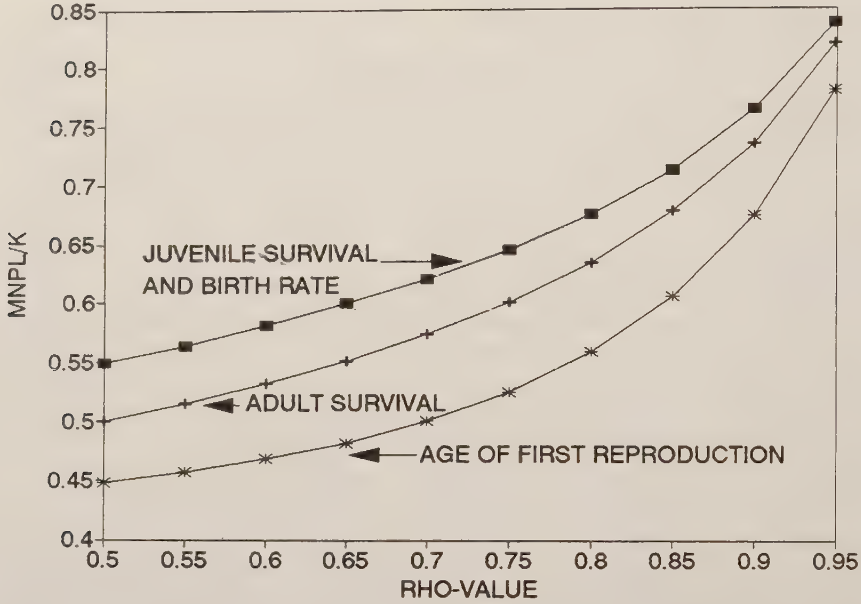

*Figure 2.* Single parameter changes (Table 1) resulting in a decrease in growth rate from $\lambda = \lambda_{max}$ to $\lambda = 1.0$. Values shown are for the odontocete model. Values for the pinniped model differed by less than 1%.

follow known empirical evidence (*i.e.*, density dependent changes are not knife-edge in form: $0.5 \leq \rho \leq 0.95$). Minimum and maximum values are given in Table 2.

## RESULTS

*Single parameter changes*—Figure 2 shows MNPL for different $\rho$-values for changes in single parameters as shown in Table 3. Results are shown for the odontocete model as values from the pinniped model never differed by greater than 1%. There are several items to note from this figure. First, as shown by Goodman (1980), not all linear density dependent changes ($z = 1$) produce a MNPL/$K$ at $K/2$ (MNPL/$K$ = 0.5). In particular, juvenile survival and birth rate produce a MNPL/$K$ of 0.55. These two rates are the same because the

*Table 3.* Demographic parameter values required to achieve specified λ by changing a single parameter from the default values in Table 1, for use in Equation 3.

| Model | $\lambda$ | $m$ | $AFR$ | $p_j$ | $p_a$ |
|---|---|---|---|---|---|
| Pinniped ($X_{N=K}$) | 1.00 | 0.232 | 10.510 | 0.245 | 0.914 |
| Pinniped ($X_{N=0}$) | 1.10 | 0.643 | 1.840 | 0.680 | 1.000 |
| Odontocete ($X_{N=K}$) | 1.00 | 0.072 | 22.681 | 0.355 | 0.961 |
| Odontocete ($X_{N=0}$) | 1.04 | 0.189 | 2.875 | 0.935 | 0.999 |

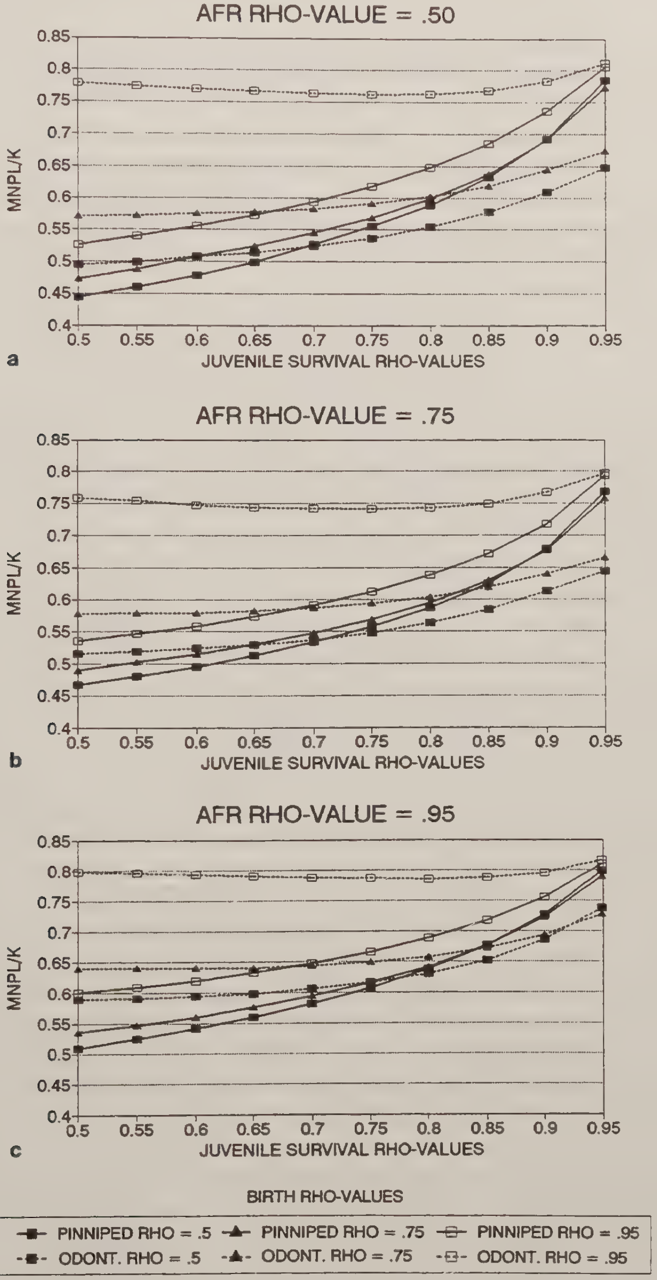

*Figure 3.* Multiple parameter changes resulting in a reduction in growth rate from $\lambda = \lambda_{max}$ to $\lambda = 1.0$. Figures a, b, and c correspond to *AFR* $\rho$-values of 0.50, 0.75, and 0.95 respectively. Pinnipeds (solid lines) and odontocetes (dashed lines) are shown for birth $\rho$-values of 0.50, 0.75, and 0.95. Lines between symbols are given for visual clarity.

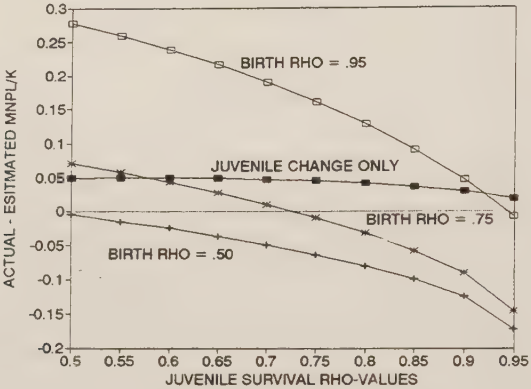

*Figure 4.* Bias in estimates of MNPL/$K$ from assuming that $\theta = z$-value for juvenile survival. To obtain the actual MNPL/$K$ value, the bias must be added to the value estimated from the $z$-value. The case shown is for odontocetes where juvenile survival is the only regulating mechanism and for three cases where *AFR* changes linearly ($z = 1$) and birth $\rho$-values are 0.50, 0.75, and 0.95.

elasticities are the same for these parameters. Recall that elasticity is the response in $\lambda$ to a proportional change in the parameter. With only one year of juvenile survival, a reduction in juvenile survival or a reduction in birth rate cause the same reduction in the number of individuals recruited into the population. The small range of MNPL/$K$ values for a given $\rho$-value irrespective of which parameter is being altered is not surprising. Even though $\lambda$ is more sensitive to $p_a$, Table 3 reveals that much smaller proportional changes in $p_a$ are required to produce the growth rate change. It may be surprising to note that even strong non-linearities ($\rho = 0.95$) do not produce MNPL/$K$ >0.85. Higher $\rho$-values will, of course, yield MNPL/$K$ values >0.85, but such highly concave functions imply no density dependent response until the population is very close to $K$. There are no empirical data to support such a knife-edge density dependent response. The final item to note is that the change required for a single parameter to accomplish all the density dependent change is often biologically unreasonable and sometimes (in the case of birth rate and *AFR*) biologically impossible. For example, in the pinniped model, AFR ranges from a minimum age (1.84) which is physically impossible to a maximum age (10.51) which is unlikely and was not observed when fur seals were thought to be near $K$ in the 1950s (Scheffer 1955). Because marine mammals produce a single offspring and have a sex ratio of 0.5, values for birth rates cannot exceed 0.5. The maximum value in Table 3 for pinnipeds ($m = 0.643$) is therefore impossible. Similar arguments can be made for the same parameters in the odontocete model.

*Changes in multiple parameters*—All combinations of *AFR,* juvenile survival and birth rates for $\rho = 0.50$–$0.95$ were investigated. Results are shown in Figure 3. Note that changes in more than one parameter yield MNPL/$K$ values which are less than those for equal $\rho$-values for changes in only a single parameter (also found in Fowler *et al.* 1980). The combination of three linear changes for the pinniped model ($\rho = 0.5$ ($z = 1$) for AFR, juvenile survival, and birth rate) actually yields an MNPL/$K$ that is less than 0.5. Comparison of the pinniped model to the odontocete model shows that MNPL/$K$ of the former to be more sensitive to changes in juvenile survival rate $\rho$-values and the latter to birth rate $\rho$-values. This is due to the differing magnitude of allowed change in these parameters (Table 2): birth rates vary more for odontocetes and juvenile survival rates vary more for pinnipeds. Thus, the models are sensitive to the minimum and maximum values. Changes in *AFR* $\rho$-values affect both models similarly when other $\rho$-values are low but have almost no effect on either when other $\rho$-values are high.

Consider the scenario where only data concerning juvenile survival were available. If we were to use the $z$-value from a fit of juvenile survival as the $\theta$ in Equation 1 how would our estimated MNPL/$K$ compare to the actual MNPL/$K$ when all birth and death functions are known? Figure 4 gives one example of bias for odontocetes. It can be seen that for a given $\rho$-value, even the sign of the bias cannot be inferred. The magnitude of the bias depends on the $\rho$-values of both the juvenile survival and birth rates. Therefore, it is not valid to infer MNPL/$K$ from the functional form of a single demographic parameter. MNPL/$K$ can be estimated either from population size estimates or from complete demographic models.

## Discussion

Although it is likely that MNPL is found at values greater than $K/2$, the argument that MNPL should be very close to $K$ (MNPL/$K > 0.8$) is unsupported. The only parameter for which empirical evidence lends credence to strong non-linearities is for juvenile survival in fur seals (Ragen 1990). Even here, many deterministic models have been used to fit the data with values for MNPL/$K$ ranging from 0.43 to 0.93 (Ragen 1990). It is clear that when data are available for marine mammals, one of the primary density dependent regulating mechanisms is age of first reproduction (Fowler 1984). There is no evidence for non-linear change for this parameter (Fowler 1984, Lett *et al.* 1981), though power is undoubtedly low. As shown in Table 3, biological constraints make the likelihood of this parameter being the sole regulatory mechanism unlikely. It is therefore likely that population growth is regulated by several mechanisms, only some of which may be non-linear (Smith and Polacheck 1981). When several parameters change in a density dependent fashion, the result is that MNPL/$K$ is less than that achieved by only a single non-linear growth rate regulating mechanism. If $z$-values for all parameters are high, MNPL/$K$ values differ very little from values estimated for MNPL/$K$ assuming $\theta = z$. On the other hand, disparities can be large if some parameter changes are linear.

The generalized pinniped and odontocete models were chosen to bracket the range of population growth rates observed in marine mammals. It may be argued, however, that these choices do not bracket the range of possible MNPL/$K$

values. Fowler (1988) argues that MNPL/$K$ is related to rate of increase per generation. The generalized models have similar rates of increase per generation. To investigate the influence of rate of increase per generation on the conclusions of this paper, we chose the most extreme outlier in Fowler's work: *Stenella*. This genus has a similar rate of increase to the odontocete model but a shorter generation time. Choice of parameter ranges were from Chivers (1992). Results were very close to the odontocete model and did not compromise the conclusions from the generalized models.

Non-linearities in population regulation mechanisms which lead to linear decreases in per capita growth rates (MNPL/$K$ = 0.5) have been noted in several laboratory systems (Barlow 1992, Kerfoot *et al.* 1985). Further, Barlow's experiment with guppies (*Poecilia reticulata*) (1992) showed highest sensitivity to density dependent somatic growth. Although mammals express determinate growth, AFR seems to be an important regulatory mechanism which may link body growth rate to population growth (Lett *et al.* 1981).

Unfortunately, we are only a little closer to defining likely ranges of MNPL/$K$. It seems likely that 0.5 < MNPL/$K$ < 0.85. For a given species, the range may be able to be reduced. For example, if we know that for fur seals $z$-values were $z = 1$, $1 \leq z \leq 3$, and $3 \leq z \leq 9$ for *AFR,* birth and juvenile survival rates respectively, then 0.58 < MNPL/$K$ < 0.73. A much more realistic fur seal model (Ragen 1990) calculated a distribution of MNPL/$K$ from simulations using permutations of possible ranges of demographic values and $z$-values. MNPL/$K$ occurred at highest frequency between 0.60 and 0.65 (corrected values; Ragen, personal communication). Unfortunately, there are few species for which we have the quantity of data available as for the fur seal.

Eberhardt (1977) proposed a general model for self-regulation in long-lived species which gave an order for age-specific density dependent responses. Such rigidity in growth regulation was questioned by a comparison of population dynamics of three species of Antarctic seals (Siniff 1984). These species, living in proximity to one another, showed varied responses which were attributed to different reactions to environmental variance. Thus, even within the Antarctic ecosystem and among closely related species, marked differences in density dependent age-specific birth and death rate responses exist. The deterministic equations discussed in this paper assume no environmental variance. Clearly, populations must evolve to respond to the stress caused by environmental changes. Marine environments change markedly over short time periods (El Niño events, fluctuations in prey availability in cold water regimes, *etc.*). Some marine mammal species are relatively fixed in space due to breeding or feeding requirements while others may be free to move over large distances to locate resources. It seems an act of faith to believe that all the likely different density dependent age-specific regulatory mechanisms would result in a narrow range of MNPL/$K$ values. The exercise in this paper has demonstrated that even if dynamics were deterministic, without knowledge about all the density dependent age-specific birth and death rates, a single value of MNPL/$K$ cannot be inferred. Distributions of MNPL/$K$ for each species given a range of parameter estimates may be more appropriate considering the current amount and quality of data.

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# The Uses of Statistical Power in Conservation Biology: The Vaquita and Northern Spotted Owl

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**Abstract:** *The consequences of accepting a false null hypothesis can be acute in conservation biology because endangered populations leave little margin for recovery from incorrect management decisions. The concept of statistical power provides a method of estimating the probability of accepting a false null hypothesis. We illustrate how to calculate and interpret statistical power in a conservation context with two examples based on the vaquita (*Phocoena sinus*), an endangered porpoise, and the Northern Spotted Owl (*Strix occidentalis caurina*). The vaquita example shows how to estimate power to detect negative trends in abundance. Power to detect a decline in abundance decreases as populations become smaller, and, for the vaquita, is unacceptably low witin the range of estimated population sizes. Consequently, detection of a decline should not be a necessary criterion for enacting conservation measures for rare species. For the Northern Spotted Owl, estimates of power allow a reinterpretation of results of a previous demographic analysis that concluded the population was stable. We find that even if the owl population had been declining at 4% per year, the probability of detecting the decline was at most 0.64, and probably closer to 0.13; hence, concluding that the population was stable was not justified. Finally, we show how calculations of power can be used to compare different*

Los Usos del poder estadístico en conservación biológica: la vaquita y el búho moteado del Norte

**Resumen:** *En conservación biológica, las consecuencias de aceptar hipótesis nulas falsas pueden ser muy severas puesto que las poblaciones en peligro de extinción dejan poco margen para revertir el efecto de decisiones incorrectas de manejo. El concepto de poder estadístico provee un método para estimar la probabilidad de aceptar hipótesis nulas falsas. Nosotros ilustramos como calcular e interpretar el poder estadístico en un contexto de conservación con dos ejemplos basados en la vaquita (*Phocoena sinus*), una marsopa en peligro de extinción, y el búho moteado del Norte (*Strix occidentalis caurina*). El ejemplo de la vaquita muestra como estimar el poder para detectar tendencias negativas en abundancia. El poder para detectar una disminución en la abundancia decrece a medida que las poblaciones se hacen mas pequeñas, y en el caso de la vaquita, es inaceptablemente bajo para el rango de tamaños poblacionales estimados. Por consiguiente, la detección de una declinación en el tamaño poblacional no debe ser un criterio necesario para decretar medidas de conservación en especies raras. En el caso del búho moteado del Norte, la estimación del poder permite la reinterpretación de resultados de análisis demográficos previos que concluyeron que la población era estable. Nosotros encontramos que aún si la población del búho moteado a estado declinando un 4% por año, la probabilidad de detectar esta declinación fue de a lo sumo 0.64%, y probablemente más cercana al 0.13%. Por consiguiente, no se justi-*

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*methods of monitoring changes in the size of small populations. The optimal method of monitoring Northern Spotted Owl populations may depend both on the size of the study area in relation to the effort expended and on the density of animals. At low densities, a demographic approach can be more powerful than direct estimation of population size through surveys. At higher densities the demographic approach may be more powerful for small populations, but surveys are more powerful for populations larger than about 100 owls. The tradeoff point depends on density but apparently not on rate of decline. Power decreases at low population sizes for both methods because of demographic stochasticity.*

*ficaba concluir que la población era estable. Finalmente, demostramos como los cálculos de poder pueden ser usados para comparar distintos métodos de monitoreo de cambios en el tamaño de poblaciones pequeñas. El método óptimo de monitoreo de las poblaciones del búho moteado del Norte depende quizas tanto del tamaño del área de estudio en relación con el esfuerzo realizado como de la densidad de los aminales. A bajas densidades, la aproximación demográfica puede ser más poderosa que la estimación directa del tamaño poblacional a partir de evaluaciones. A mayores densidades la aproximación demográfica puede ser más poderosa para poblaciones pequeñas, pero las evaluaciones son más poderosas para poblaciones de mas de 100 búbos. El punto de relación (tradeoff) depende de la densidad pero aparantemente no depende de la tasa de declinación. Para tamaños poblacionales bajos, el poder decrece para ambos métodos debido a la estocasticidad demográfica.*

## Introduction

Consider the following scenario: a species is declining in abundance, and we have gathered data that may show that a certain pollutant is responsible. We evaluate the data with an appropriate statistical test, but the null hypothesis (of no effect) is not rejected. The result? Without statistically significant evidence that the pollutant is harmful, it is unlikely that any action will be taken to eliminate or reduce the pollutant.

Now consider the following question: If the pollutant does have a harmful effect, what is the probability that we would have detected it? The answer is clearly of central importance, yet this probability, called statistical power, is rarely calculated. The reasons why power has been largely ignored lie partly in the historical development of hypothesis testing and partly in the extra effort required to make power calculations. We believe that a consideration of power is critical in many conservation issues, however, and that every conservation biologist should be familiar with the concept of statistical power. An awareness of statistical power is particularly important in conservation biology because the consequences of incorrect decisions can be severe: the extinction of a species. A medical analogy may be helpful. Consider a medical test that determines whether a patient has some deadly disease. Physicians are properly less concerned with a false positive (concluding that the patient has the disease when she does not) than with a false negative (concluding that the patient does not have the disease when she does). Conservation biologists deal with the health of species and ecosystems and should be similarly concerned with false negatives.

The importance of statistical power is becoming more widely appreciated in many fields of biology. A number of papers in recent years have pointed out the importance of considering power in ecological studies (Quinn & Dunham 1983; Toft & Shea 1983; Rotenberry & Wiens 1985; Peterman 1990*a*). Consideration of statistical power is an integral part of proper experimental and sampling design (see Eberhardt & Thomas [1991] and Andrew & Mapstone [1987] for recent examples). Explicit calculations of power are increasingly being utilized in applied ecology, for example in wildlife ecology (Skalski et al. 1983; Halverson & Teare 1989), insect demography (Solow & Steele 1990), toxicology (Hayes 1987), fisheries (Peterman & Bradford 1987; Peterman 1990*b;* Cyr et al. 1992) marine mammal studies (de la Mare 1984; Holt et al. 1987; Forney et al. 1991), and ecosystem and population monitoring (Skalski & McKenzie 1982; Hinds 1984; Gerrodette 1987, 1991; Green 1989).

There are two main ways that power calculations can be applied in conservation biology. First, before collecting data, study designs can be evaluated in terms of their ability to yield significant results. How large must samples be? How many years will it take? And (ultimately) how much money must we spend? Calculating power for study designs can help answer these questions. We illustrate this use of power by considering the ability of line-transect surveys to show a decline in abundance of a rare species the vaquita (*Phocoena sinus*), a porpoise. We illustrate evaluation of two monitoring designs with the Northern Spotted Owl (*Strix occidentalis caurina*) by comparing demographic to survey methods for detecting declines in abundance. Second, after data have been collected, calculations of power can help interpret the results, particularly when the null hypothesis has not been rejected. We illustrate this use of power in our second example by evaluating the strength of Lande's

(1988) conclusion that the Northern Spotted Owl was not declining in abundance.

### Statistical Hypothesis Testing

The dominant paradigm for hypothesis testing, as described in most introductory textbooks, involves:

(1) choosing null and alternative hypotheses;
(2) devising and carrying out an experiment or sampling program designed to distinguish between the two alternatives;
(3) computing an appropriate statistic that summarizes the property to be compared;
(4) determining whether the observed value of the statistic has a probability of occurrence less than a pre-chosen level of significance $\alpha$; and
(5) if it does, rejecting the null hypothesis in favor of the alternative, or if it does not, retaining the null hypothesis.

The final step involves a yes/no decision about the falsity of the null hypothesis, and the possible logical outcomes of this procedure are often displayed in the form of a simple table (Table 1). Two types of error are possible. If the null hypothesis is true but is rejected, a Type 1 error occurs with probability $\alpha$; a correct decision is made with probability $1 - \alpha$. If the null hypothesis is false but is not rejected, a Type 2 error occurs with probability $\beta$. Statistical power is the probability that the null hypothesis will be rejected when it is false. Hence, power is the probability that we reach a correct decision when the null hypothesis is false, and is calculated as $1 - \beta$ (see Table 1).

Before proceeding to our examples, two brief comments on this procedure are in order. First, the evaluation of data relative to a significance level $\alpha$ (commonly 0.05) depends on naming a specific null hypothesis, but the alternative hypothesis may be nonspecific. For example, we might have as our null hypothesis $H_o$: mean of population $A$ = mean of population $B$, but the alternative may be the non-specific $H_A$: mean of $A \neq$ mean of $B$. On the other hand, the calculation of $\beta$ and power $(1 - \beta)$ requires that a specific alternative be given—for example, $H_A$: mean of $A = \frac{1}{2}$ (mean of $B$). Power has meaning only in relation to a specific alternative hypothesis, and different alternatives result in different values of power.

**Table 1. Possible logical outcomes and types of statistical error when testing a null hypothesis $H_o$.**

| | *Result of statistical test* | |
|---|---|---|
| | Do not reject $H_o$ | Reject $H_o$ |
| $H_o$ is true | Correct decision made with probability $1 - \alpha$ | Type 1 error ($\alpha$) made with probability $\alpha$ |
| $H_o$ is false | Type 2 error ($\beta$) made with probability $\beta$ | Correct decision made with probability $1 - \beta$ (power) |

*The power of a test is the probability that* $H_o$ *will be rejected when* $H_o$ *is false.*

Second, although the above procedure is well established and our discussion applies strictly within the framework of this procedure, there are other methods of testing statistical hypotheses. We may also decide between two hypotheses on the basis of likelihood ratios (Berger & Wolpert 1985) or Bayesian methods (Box & Tiao 1973; Berger 1988; Howson & Urbach 1989). Barnett (1982) presents a general discussion of statistical inference.

### Example 1: *Phocoena Sinus*

The vaquita is a small porpoise that occupies a limited range in the northern Gulf of California, Mexico. The status of the porpoise is listed as endangered by the United States Endangered Species Act. Although very little is known about vaquita, one can unequivocally state that the species is rare. In the first dedicated survey in 1976, only two sightings were made in 1959 km of trackline (Wells et al. 1981). From 1986–1988 a total of 3236 km of boat and aircraft surveys resulted in 51 sightings of 96 individual porpoise (Silber 1990). The surveys were not random, but tended to concentrate in areas with highest sighting probability. Barlow (1986) estimated 50–100 individuals as a rough lower limit for the population, noting that available data could not be used for an upper limit. In September of 1991, experimental aerial surveys were conducted to assess the viability of this method for estimating abundance (Barlow et al. 1993). A single sighting of two animals was made in 1143 km of random transect lines. While estimates from so few data are crude, it is likely that there are fewer than 1000 vaquita remaining. There is, meanwhile, substantial mortality occurring due to gill net fisheries. A conservative estimate of the number of animals killed in gill nets is 102 (Vidal 1990). Of these, 79 have occurred since 1985 and 72 were in nets for *Totoaba macdonaldi*, a large sciaenid fish which is itself endangered.

Are surveys able to tell us if the vaquita population is declining in abundance? To investigate this question we created a simple simulation of a line-transect survey (Appendix 1). The results showed that an intensive survey covering virtually all known vaquita habitat could provide an accurate estimate of population size, but that the precision of that estimate strongly depended on population size (Table 2). On theoretical grounds the

**Table 2. Results of simulated line-transect surveys for the vaquita, *Phocoena sinus*.**

| *Actual population size* | *Mean estimate of abundance* | *Coefficient of variation of estimate of abundance* |
|---|---|---|
| 250 | 253 | 0.387 |
| 500 | 495 | 0.283 |
| 1000 | 1015 | 0.209 |
| 2000 | 2005 | 0.138 |
| 4000 | 3999 | 0.100 |
| 8000 | 8010 | 0.071 |
| 16,000 | 16,020 | 0.050 |

*Mean and coefficient of variation were computed from 1000 simulated surveys at each population size.*

variance of a line-transect estimate was expected to be proportional to abundance (Burnham et al. 1980). This relationship was confirmed when we regressed the coefficient of variation of our simulated abundance estimates ($CV$) (Table 2, column 3) against the inverse of the square root of population size ($N$) (Table 2, column 1) to give

$$CV = 6.248\left(\frac{1}{\sqrt{N}}\right) \qquad (r^2 = 0.995, p \ll 0.001). \tag{1}$$

The importance of Equation 1 lies in the fact that our ability to detect a decline in population size depends strongly on the precision of the estimate of population size. As $N$ decreases, $CV$ increases, and the probability that a series of surveys will indicate a significant negative trend decreases. This is a specific example of the more general relationship between power, the size of the "effect" we want to detect ($ES$, for effect size; see Cohen 1988), and the variability ($V$) in our data. Very roughly, we can summarize the general relationship by

$$Power = f\left(\frac{ES - T_{1\text{-}\alpha}}{V}\right).$$

In words, power is an increasing function of effect size (bigger effects are easier to detect), a decreasing function of the test statistic $T_{1\text{-}\alpha}$, which itself negatively depends on $\alpha$ (thus, higher $\alpha$ leads to higher power), and an inverse function of variability (more variable data mean lower power). In the specific case of a series of surveys, the probability of obtaining a significant negative trend (that is, the power, or $1\text{-}\beta$) can be approximated by the following relationship (Gerrodette 1987):

$$z_\alpha + z_\beta \le \ln\lambda\left(\sqrt{\frac{n^2(n+1)(n-1)}{12\sum_{i=1}^{n}\ln\left(\frac{CV_1^2}{\lambda^{i-1}}+1\right)}}\right) \tag{2}$$

where $z_x$ = the $x$ quantile of the standard normal distribution,
$\alpha$ = the probability of Type 1 error,
$\beta$ = the probability of Type 2 error,
$\lambda$ = the factor of decrease between surveys ($0 < \lambda < 1$),
$n$ = the number of surveys, and
$CV_1$ = the coefficient of variation of the population estimate at the initial population size.

Thus, the probability of obtaining a significant negative trend depends on the precision of the surveys ($CV$), how rapidly the population is declining ($\lambda$), the number of surveys ($n$), as well as the significance level of the test ($\alpha$). Equation 2 assumes that the population is declining exponentially, that line-transect (or similar sighting per unit effort) data are used to estimate abundance, and that a one-tailed test (for a decline) is used. Note that because the relationship between $CV$ and $N$ is included in the derivation of Equation 2, it is necessary only to give the initial $CV$ for any particular power calculation. Also note that, if anything, the approximation represented by Equation 2 *over*estimates power (Gerrodette 1991); this makes the following pessimistic conclusions about our ability to detect trends all the stronger. As applied to the endangered vaquita, the results may be expressed in several ways:

(1) As population size decreases, so does our ability to detect the decrease (Fig. 1A). Five annual surveys are unlikely to detect a 5%/year population decline for any population size less than 3000 vaquita. If we conduct five biennial surveys, the probability of detecting a 5%/year decline in the vaquita population (a 40% decline over the ten-year period) is 0.81 if the initial population is 3000 porpoise but only 0.45 if the initial population is 1000. Even under the most intensive effort shown in Fig. 1A (10 annual surveys), the power of detecting a 5%/year decline is acceptable (if we define acceptable as $\beta \le \alpha$) only if the vaquita population is larger than 2300 animals. The actual vaquita population is almost certainly less than that (Silber 1990). If the vaquita population size is in the low hundreds of animals, as the best available data indicate, the most likely outcome of *any* surveys will be a nonsignificant trend, even when the population actually is declining.

(2) As population size decreases, the detectable rate of decline (that is, the minimum rate of decline that could be detected with a given amount of survey effort) increases (Fig. 1B). For example, if there were 300 vaquita, even the most intensive survey effort (10 annual surveys) gives a minimum detectable rate of decline of 18%/year ($\lambda = 0.82$). This rate implies a reduction of 86%, from 300 to 42 vaquita, during the ten-year study period, which is clearly unacceptable. Less frequent sur-

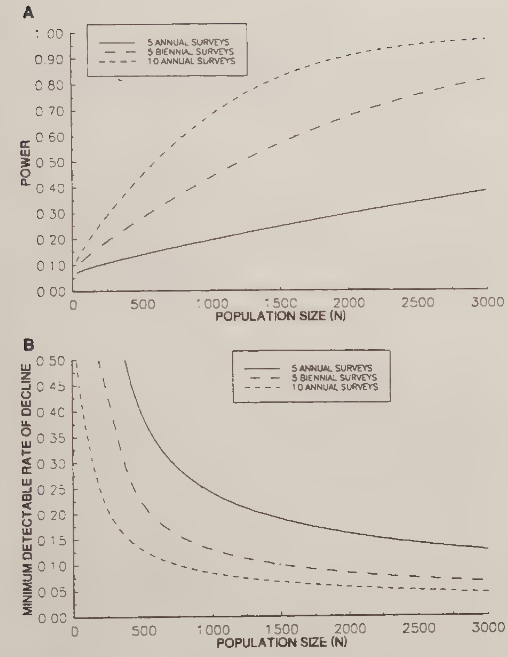

*Figure 1. Results of a power analysis for a simulated vaquita survey (Appendix 1). Values are computed from Equation 2 using α = 0.05 (1-tailed) for various numbers of surveys (n), as a function of initial population size (N). (A) Power to detect a 5%/year decline (λ = 0.95). (B) Minimum detectable annual rate of decline (1 − λ) with high power (α = β = 0.05).*

veys (five biennial surveys) or a shorter study period (five years) result in minimum detectable rates of decline that are even higher (Fig. 1B).

The management implications of this analysis are clear. While there may be important reasons for undertaking vaquita surveys (and we believe there are), determining whether the vaquita population is declining is not one of them. Even worse would be to predicate conservation efforts on whether the surveys indicate a decline. Simply put, if we were to wait for a statistically significant decline before instituting stronger protective measures, the vaquita would probably go extinct first.

### Example 2: *Strix Occidentalis Caurina*

Northern Spotted Owls, found in western North America, depend on old-growth forests (Thomas et al. 1990). Concern is prompted because their habitat has been greatly reduced and fragmented by logging, and this habitat loss is expected to continue. Recent studies have demonstrated declines in several owl populations (Thomas et al. 1990). Northern Spotted Owls are long-lived, territorial animals. Because of their relatively sedentary adult life, natural mortality in adults can be accurately assessed by banding studies. Most juveniles are forced to disperse some distance to claim a vacant territory. Estimating juvenile mortality, therefore, has proven difficult. Current estimates place lower and upper bounds for Northern Spotted Owls at 2000 and 6000 individuals (Thomas et al. 1990). Because logging of old-growth forest is continuing, determining the dynamics of the owl population is complex. Current efforts to estimate population growth rates target a snapshot estimate of whether populations are declining while habitat is being destroyed (Anderson et al. 1990). Here we address a simpler question: "Given a static habitat, can we detect a decline in owl abundance?"

## Power to Detect a Decline by Demographic Analysis

Several studies have attempted to determine whether Northern Spotted Owl populations were declining by performing a demographic analysis (Lande, 1988; Noon & Biles 1990). As first laid out by Lande (1988), this approach models the population's dynamics as

$$N_t = N_0\lambda^t, \tag{3}$$

where $N_t$ is population size at time $t$, and $\lambda$ is the geometric factor of change. We can estimate $\lambda$ by solving the characteristic equation using a simplified three-category age structure (Noon & Biles 1990; Thomas et al. 1990) (note that this equation and those used for variance differ from Lande [1988] and Caswell [1989]):

$$\lambda^2 - s\lambda - s_0 s_1 b = 0, \tag{4}$$

where

$s_0$ = survival rate from age zero to one,
$s_1$ = annual survival rate of sub-adults,
$s$ = annual adult survival rate, and
$b$ = annual birth rate.

Estimates of these vital rates are available (Table 3). As Lande notes, because $\lambda^3 b \geq 0$, the real positive solution of this equation must be such that $\lambda \geq s$; that is, the rate of decline cannot be less than the adult survival rate. In other words, if all recruitment into the adult population were to cease and the survival rate of territory-holding adults were to remain constant, $\lambda$ would be 0.94.

Lande concludes: "The estimated value of $\lambda = 0.961$ is less than twice its standard error from 1.0 and is therefore not significantly different from that for a stable pop-

**Table 3. Demographic parameters for the Northern Spotted Owl used by Lande (1988).**

| *Parameter* | *Estimate* | *Sample size* |
|---|---|---|
| $s_0$ | 0.108 | 179 |
| $s_1$ | 0.710 | 7 |
| $s$ | 0.942 | 69 |
| $b$ | 0.240 | 438 |
| $\lambda$ | 0.961 | |

*Sample size is the number of individuals used to estimate the parameter. We have combined Lande's $s_0$ (the predispersal survival rate) and $s_d$ (survival rate of dispersers) into a single term for survivorship through the first year of life ($s_0$), as has been done in subsequent analyses (Anderson et al. 1990; Thomas et al. 1990).*

ulation, supporting the contention that the population currently may be near a demographic equilibrium." Although these data cannot reject the null hypothesis using Lande's equations, the data do not support the latter contention. A value for λ of 1.000 cannot be rejected, but the same could be said for λ = 0.920; it also cannot be rejected. In fact, given Lande's own assumptions about the distribution of λ, λ = 0.920 is just as likely as λ = 1.000, and the most likely value is the mean, λ = 0.961. Lande properly states that the confidence interval on the estimated λ includes 1000, but the data hardly support the contention that λ = 1,000.

To conduct a power analysis, we consider the following question: If λ = 0.961 (a decline of 4%/year), what is the probability of rejecting a conclusion of a stable population (λ = 1.000)? We generated a distribution for λ = 0.961 and λ = 1.000 (Fig. 2A). Details of the simulations are given in Appendix 2. The histograms in Fig. 2A represent the spread of values for λ that we would expect to obtain if we were to repeat our measurement of Northern Spotted Owl demographic parameters many times, under the assumption that the parameters themselves were constant. Different values of λ result from sampling error in the estimation of demographic parameters. The histograms show that were the true λ = 0.961, we would reject the hypothesis that λ = 1.000 for 64% of all estimates of λ (with α = 0.05). Power, in other words, is 0.64. Power can be increased up to 0.84 at the cost of accepting an α level as high as 0.25 (Table 4 column with "sampling error only"). In general, though, we have little power to distinguish between these two distributions even though a decline of 4%/year would lead to loss of a third of the population in ten years. Lande's (1988) procedure of computing a confidence interval on the observed λ has even lower power: 0.08 (Table 4). In other words, given a population actually declining at 4%/year, Lande's procedure would conclude that λ was not significantly different from 1.000 92% of the time. This makes weak indeed the claim that the data support λ = 1.000.

Even this analysis is optimistic, however, because it considers only the sampling error that arose in the estimation of the demographic rates. The rates were estimated by pooling data over years to obtain a single estimate with the variance in mortality calculated from the binomial distribution. It is most likely, however, that owl populations experience environmental variability that translates into year-to-year variability in the demographic parameters and the population growth rate. For the Tawny Owl (*Strix aluco*), a closely related species, owls did not breed in years of low prey abundance, a harsh winter reduced the adult population by half, and there was a clear ceiling on the number of territories, which must limit recruitment (Southern 1970). To generate more realistic distributions of λ for the Northern Spotted Owl, we used the variance of birth and death

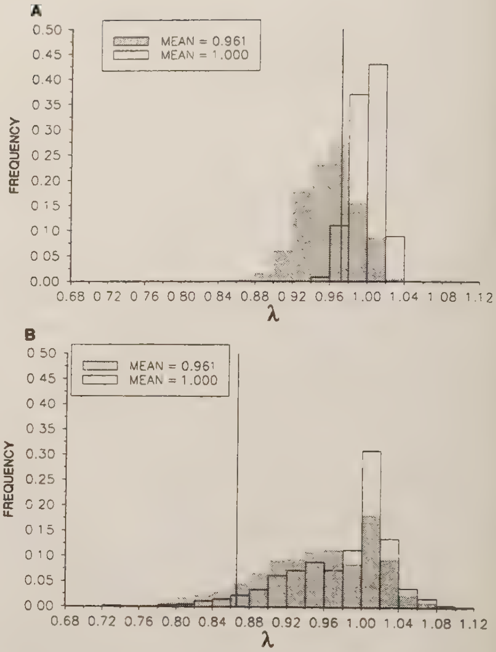

*Figure 2. (A) Histograms of 1000 simulations using Lande's (1988) data. Mean data rates are fixed, and variance is due to sampling error (binomial variance). The mean and variance of birth rates (Barrowclough & Coates 1985) also remained fixed. The vertical line is the α = 0.05 critical value below which lies the 5% of the unshaded histogram with mean λ = 1.0. Values less than those would be rejected as not having come from the null distribution. (B) Histograms as in (A), with environmental variance estimated from variance in birth and death parameters estimated from the Tawny Owl.*

**Table 4. Power $(1 - \beta)$ estimated by Monte Carlo simulation to detect a 4%/year decline under two different assumptions about variance: variance is due to sampling error only, and variance is due to environmental variation in addition to sampling error.**

| | Power | |
|---|---|---|
| | *Sampling error only* | *Including environmental variation* |
| Simulations with $\alpha = 0.05$ | 0.644 | 0.116 |
| Simulations with $\alpha = 0.10$ | 0.726 | 0.211 |
| Simulations with $\alpha = 0.25$ | 0.843 | 0.432 |
| Lande's Criterion | 0.084 | 0.049 |

*The Lande critical value is the mean plus twice the standard error of λ as defined by Lande (1988). The distributions are shown in Figs. 2a and 2b.*

rates from the Tawny Owl study in the same Monte Carlo simulations (Appendix 2). The resulting distributions (Fig. 2B) are more similar to each other than when only sampling error is considered (Fig. 2A). This means that the null and alternative hypotheses will be even more difficult to distinguish from each other, and that the power to detect a 4%/year decline ($\lambda = 0.961$) will be dramatically lower (Table 4, column "including environmental variation"). Because of small sample sizes, the likely outcome of the comparison of data from any two years will be an inability to distinguish between estimated parameters, but this does not mean that no environmental variance exists. On the other hand, pooling data over years may lead to unrealistically small variances that give a false picture of the precision of the data. Separation of sampling and environmental variance can be a complicated statistical issue; replication and analysis of model fit can aid in their estimation (see Burnham et al. 1987: Part 4).

## Comparison of Two Methods of Monitoring Population Size

In this final section, we use a power analysis to compare two methods of monitorng Northern Spotted Owls for possible declines in population size. To determine whether a population is declining, we could attempt to determine if $\lambda = 1.0$ from estimates of birth and death rates, as considered in the previous section, or we could attempt to estimate population size directly over several years and to determine whether the estimates indicated a decline over time. We will call the former approach the demographic method and the latter the survey method. The question is, given a fixed amount of effort, which method has the greatest probability of detecting a decline in population size?

Although we use the Northern Spotted Owl as an example, we emphasize that the following comparison is presented as an heuristic example of using power analysis to compare study designs. It shows how different study designs could, before time and money are invested, be evaluated for their ability to yield useful information. It is not intended as a recommendation for the study of any particular owl population, or as a criticism of any past or present owl studies. In particular, our analysis does not consider the nonequilibrium conditions that currently exist due to timber harvest (Lamberson et al., in press).

The comparison of the two methods depends on several assumptions: the amount of time and money available, the probability of detecting an owl from a given distance, and the relation between population size and capture rate. We have attempted to use reasonable values based on past studies (Appendix 2). The details of our results depend on the specific values we have chosen for, say, the amount of banding effort, but this does not detract from the generality of the approach. Because Northern Spotted Owls are territorial, we assume that owls occur at some given density in a potential study area, and thus that the choice of a study area determines the size of the study population.

First, for the demographic method, we simulated the estimation of λ from banding studies and estimated the probability (power) of concluding that $\lambda < 1.0$ for several different true values of λ (Appendix 2). The results show, as expected, that power increases as λ decreases (solid curves, bottom to top in Fig. 3). Less obvious is that, for a given λ, power generally declines as the size of the study population increases (solid curves in each graph in Fig. 3). If we have chosen to monitor a large population (area), the proportion of the population captured for banding will be small, the variance of the estimates of birth and death rates and hence, λ will be high, and the ability to reject the null hypothesis that $\lambda = 1.0$ (power) will be low. Thus, we do not want to choose too large a study population relative to the planned banding and capturing effort. However, we also do not want to choose too small a study population. At very small population sizes, power is affected by variability due to stochastic demographic effects. If we choose a very small study population, we may be able to monitor every individual owl, but power decreases because the probability decreases that the actual number of owls surviving will exactly equal the survival probability (left ends of solid lines in Fig. 3). For example, if the adult survival rate is 0.96 and our study population consists of 10 adult owls, it is impossible that 9.6 will survive. The power to detect $\lambda < 1.0$ is therefore maximized at some intermediate value of study population size. For the amount of effort assumed in these simulations, the optimum population size (study area) to choose for a banding study to estimate λ is about 60

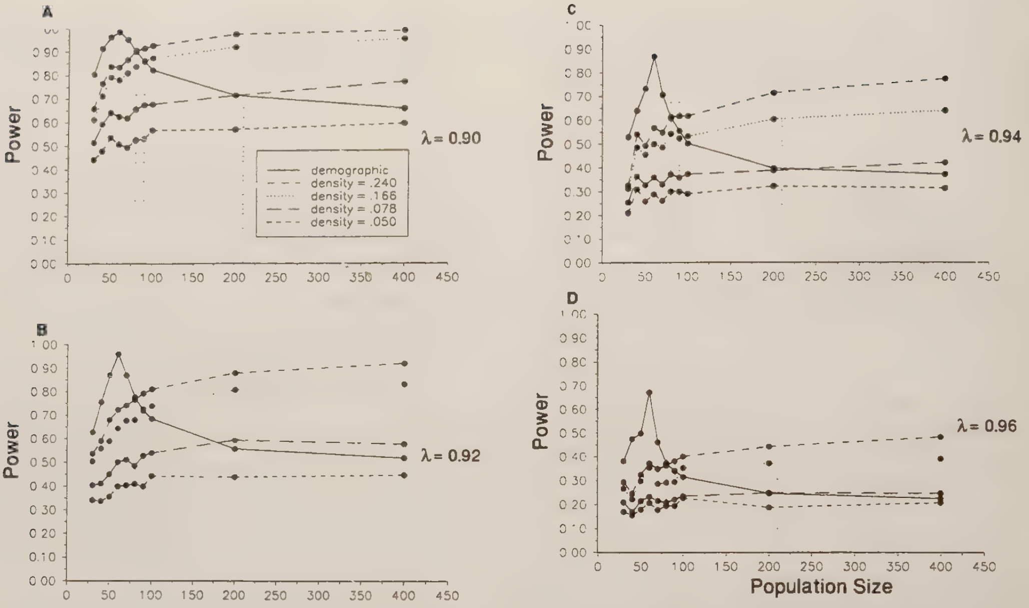

*Figure 3. Comparison of power of two methods of monitoring declines in Northern Spotted Owl population size. Solid lines plot power for the demographic approach, and broken lines plot power of line-transect surveys at four owl densities, for the following population growth rates (λ): (A) 0.90, (B) 0.92, (C) 0.94, and (D) 0.96. Dots indicate power calculated from simulations. Connecting lines are linear interpolations. Vertical dotted lines running through figures A–D show that the tradeoff point where power from line-transect techniques exceeds the power from demographic techniques is not affected by the population growth rate.*

adult owls (Fig. 3). This is approximately the size of the population chosen for an intensive banding study in northern California (Franklin et al. 1990).

Second, for the survey method, we simulated the estimation of population size from a line-transect survey and estimated the probability (power) of concluding that there was a downward trend in population size over a five-year period (Appendix 2). The results show that, as for the demographic method, power increases as λ decreases, and that power declines at small population sizes due to stochastic demographic effects (dashed lines, bottom to top in Fig. 3). In contrast to the demographic method, however, the power of the survey method does not decline with increasing size of the study population. Power increases with population size up to the point where stochastic demographic effects become negligible and is constant thereafter. Also in contrast to the demographic method, power is an increasing function of owl density (dashed lines in each graph of Fig. 3). These differences occur because the precision of an abundance estimate from a survey depends primarily on the number of animals seen on the survey, and, other things being equal, on the density.

Comparing the two methods in Fig. 3 shows several interesting features. First, for the lowest density of owls considered here (0.050 owls/km$^2$), the demographic method is always the more powerful design. Thus, were we considering monitoring Northern Spotted Owl populations in a low density area, such as the Olympic peninsula in Washington (Thomas et al. 1990), we should choose the demographic method regardless of size of study area. For higher densities, there is a tradeoff point where the survey method becomes more powerful than the demographic method as study population size increases. The tradeoff point is approximately 80 owls for the highest density (0.240 owls/km$^2$), 90 owls for the next highest density (0.166 owls/km$^2$), and 210 owls for the third highest density (0.078 owls/km$^2$). These tradeoff points do not depend on the actual rate of decline (which is fortunate since this is the quantity we ultimately want to estimate!). Thus, if we were considering monitoring Northern Spotted Owl populations in areas of moderate to high density of owls and the study area was thought to contain at least 100 owls, we should choose the survey method as the more powerful design to detect a population decline.

## Conclusion

In conservation biology, as in any scientific research, experiments should be carefully designed to answer the most pressing questions. However, the need for careful experimental design is particularly important in conservation biology because (1) the crisis nature of many situations may not allow time for research to be repeated, (2) money is always in short supply, so it is imperative to use it in a way that will yield the most information, (3) the research activity itself may have some effect on the population, which should be minimized, and (4) the precarious nature of many populations allows little margin to recover from incorrect decisions. An analysis of power is an integral part of good experimental design (Winer 1971). The examples provided here have been chosen to demonstrate how power analysis can allow us to (1) decide whether the proposed research can answer our question, (2) choose among alternate experimental designs, and (3) interpret the results in such a way that is is clear exactly what we can and cannot state given our data.

Although awareness is increasing, statistical power is often ignored in ecological studies (Peterman 1990*a*). A recent review in the field of fisheries biology pointed out that of 408 fisheries papers that reported at least one failure to reject the null hypothesis, only one calculated the probability of making a Type 2 error (Peterman 1990*b*). Our informal survey of past issues of *Conservation Biology* indicate a similar lack of reporting power. We contend that a consideration of power is especially important in conservation biology. Both the vaquita and Northern Spotted Owl examples demonstrate why it is insufficient merely to state that the data failed to reject the null hypothesis. With small populations, failure to reject the null hypothesis may often result from inadequacies in the data rather than from any evidence concerning the falsity of the hypothesis. Such inadequacies may be due to small sample sizes, stochastic demographic effects, or both. In this paper we have particularly illustrated the use of power for detecting changes in population size. However, there are many other situations in conservation biology for which a power analysis is appropriate. For example, consider the problem of defining suitable habitat. This could arise in the context of designing wildlife reserves (what areas are most important?) or in altering habitat for the benefit of rare species (have restoration or mitigation efforts been successful?). We might be comparing abundance, survival rates, behavior, or other characteristics of populations in several areas. In these situations a Type 2 error would lead to the designation of less suitable habitat in a reserve or to the false conclusion that restoration was being successful.

What level of power should we consider acceptable? There is no simple answer to this question. Although there is a generally accepted level of Type 1 error ($\alpha \leq 0.05$), there is no such generally accepted standard for Type 2 error. Furthermore, the relative importance attached to these two kinds of statistical error depends on one's perspective. Consider again the example of the putative pollutant given in the introduction. A manager of a factory producing the pollutant would be most concerned with minimizing Type 1 error—that is, with minimizing the probability of deciding that the pollutant is responsible when it really is not The result of this incorrect conclusion may be the unnecessary installation of costly equipment. A conservation biologist would also not want to make a Type 1 error, but for a different reason: loss of scientific credibility. However, biologists should be even more concerned about making a Type 2 error—that is, of deciding the pollutant is not responsible when it is—because the result of this incorrect conclusion may be the extinction of the species in question. Because Type 1 and 2 errors result in quite different consequences, weighing their relative costs can be a complex and contentious undertaking. We do not disparage its difficulty. Our point here is that a discussion of the costs cannot proceed without a recognition and calculation of the probability of Type 2 error and its complement, power.

Because of the critical nature of management decisions in conservation biology, we should also consider where the burden of proof should lie. Should scientists be required to show that a population is declining before a negative impact (a direct kill or habitat destruction) can be controlled? One alternative is to require that the party affecting the population show, with high power, that the impact will have no effect before it is allowed (Peterman 1990*a*). A precedent for this approach already exists. Before a new drug is approved, the U.S. Food and Drug Administration puts the burden of proof on the drug industry to show that the drug is *not* harmful (Belsky 1984). Another approach might be to take as our null hypothesis, on the basis of past experience with this or a similar species, that there *will* be an effect, and that the impact cannot be allowed unless this null hypothesis can be rejected. For rare species, such as the vaquita, we have seen that it is inappropriate to require proof of a decline before reductions in the population are halted. An alternative approach may be to require proof that the population is not declining either through survey techniques or by demonstrating that recruitment exceeds removal. Consideration of power may thus cause us to rephrase our hypotheses so that they are appropriate for each conservation problem.

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## Appendix 1

### Porpoise Simulations

Vaquita (*Phocoena sinus*) are very similar in their sighting characteristics to the harbor porpoise, *P. phocoena*. We therefore used the sighting detection function for harbor porpoise in calm conditions (Beaufort 0 and 1) (Barlow 1988) in our simulations of a ship-based vaquita line-transect survey. Sightability was not affected by group size since vaquita are found only in small groups (Silber 1990); the distribution of group size was taken from Silber's work. We assumed that groups of porpoise were randomly located within their range. The range of the species was considered to be approximately 4900 $km^2$, which lies between the 20- and 40-meter depth contours in the northern Gulf of California; nearly all sightings of vaquita have been made in this habitat (Silber 1990; Vidal 1990). For complete coverage we set track lines 5 km apart (see part one of the simulation protocol). For the given area this would yield 980 km of survey, which at a survey speed of 15 km $hr^{-1}$ would require approximately eight days of eight hours of survey under perfect conditions. Obtaining these hours would take several weeks, which seemed a likely amount of effort.

To generate statistics for a vaquita population estimate, we repeated the following procedure 1000 times: (1) a distance from the track line was chosen from a uniform distribution from zero to half the distance between transect lines (2500 m); (2) group size was chosen randomly from the group size distribution; (3) simulation population size was incremented; (4) the probability of being sighted at that distance was determined from the sighting detection function; (5) animals seen were added to the abundance estimate; (6) steps 1 to 5 were repeated until the simulation population size equaled $N$. The procedure was repeated for $N$ = 250, 500, 1000, 2000, 4000, 8000, and 16,000. Number of animals seen was an index of population size. Because sighting conditions were assumed to be constant, the line-transect estimate of porpoise abundance was directly proportional to the number of vaquita seen. The mean and coefficient of variation of abundance in Table 2 were computed from this index of abundance.

The simulations for this example are intentionally simplistic and have not taken into account many sources of error that would be found in a real survey. For example, we allow for no error in estimation of group size, use data only from the best sighting conditions and from a large ship that is likely to be a better sighting platform than will be available for a survey of vaquita. Each of these simplications have reduced variance. The result is a best-case scenario for power to detect a population decline.

## Appendix 2

### Owl Simulations

The distribution of λ with sampling error only (Fig. 2A) was generated by repeating the following steps 1000 times: (1) each survival rate was calculated by doing $n$ (sample size for that age category) repeats of a trial where a randomly chosen value from a uniform distribution from zero to one determined the fate of the individual according to the survival probability for that age category; (2) the birth rate was determined by finding the mean of $n$ trials (sample size for birth rate) where the birth number was chosen from a normal distribution with the mean $b$ and variance of $1.2b$ (Barrowclough & Coates 1985); (3) the $\lambda$ for this set of demographic parameters was computed by solving Equation 4. We followed this procedure using the demographic parameters in Table 3 (mean $\lambda = 0.961$), with all parameters multipled by 1/0.961 (mean $\lambda = 1.000$).

The same Monte Carlo techniques were used to generate the distribution of $\lambda$ with environmental variation (Fig. 2B), except that, for each time-step demographic rates were chosen from normal distributions with the following means and standard deviations: $s_0$: 0.112, 0.615; $s_a$: 0.739, 0.265; $s$: 0.980, 0.080; $b$: 0.250, 0.640. These parameters were calculated from the Tawny Owl data (Southern 1970). Birth rates were constrained to be non-negative, and survival rates were constrained to lie between zero and one.

Simulations for Fig. 3 produced distributions for both the demographic technique and the line-transect technique. Four possible adult survival rates ($s$) were chosen: 0.90, 0.92, 0.94, 0.96. Birth rate was held constant and juvenile survival was adjusted to obtain $\lambda = 1.000$. These parameters were used to obtain the distribution for the null hypothesis. The alternate hypothesis assumed no recruitment, that is $s_0 = 0$. Thus the rate of decline was $1 - s$. The following assumptions were used for the line-transect portion: (1) probability of sighting ($p$) with distance is 0–100m, $p = 1.00$; 101–200m, $p = 0.60$; 201–400m, $p = 0.45$; 401–500m, $p = 0.25$; 501–600m, $p = 0.15$, 601–700m, $p = 0.05$ (based on buteos) (Anderson et al. 1985); (2) densities are estimated from home-range data from radio-tagged owls as presented in Thomas et al. (1990)—for the Olympic peninsula, Washington (0.050 owls/km$^2$), Washington Western Cascades (0.078 owls/km$^2$), Oregon Western Cascades (0.166 owls/km$^2$), and northern California (0.240 owls/km$^2$, Franklin et al. 1990). Assumptions for the demographic portion were as follows: capture rate = $63.7/N$ or 1.0 for $N < 63$ (based on capture data in Franklin et al. [1990]); all owls are of equal ease of capture, and capture rate is not dependent on density. Effort was held constant at the level reported in Franklin et al. (1990), which gave a capture probability of 0.91 for a population of approximately 70 owls. The average effort of 400 hours/year was translated into line-transect effort by assuming a survey speed of 1.6 km/hour. For both techniques, it was assumed that only females were counted. The following steps were repeated 10,000 times: (1) the number of owls for a five-year period is determined by allowing each individual to die and/or give birth stochastically (as in previously described simulations); (2) number of owls seen each year is determined stochastically according to the detection function; (3) the log of the number seen each year is regressed linearly against time to obtain the slope, which is the estimated rate of decline; (4) demographic parameters are computed for years 2–5 as (1) survival rate of adults = (adults captured time $B$)/[(adults captured time $A$) + (juveniles captured time A)]; (2) survival rate of juveniles = (juveniles captured time $B$)/(newborns captured time $A$); (3) birth rate = (newborns captured time $B$)/(adults captured time $A$); (5) the means of the four estimated death and birth rates (for years 2–5) are used to calculate $\lambda$.

For the case of $\alpha = 0.05$, the critical value is the lower fifth percentile of the null hypothesis distribution. Power was estimated for the alternate (declining) hypothesis by the fraction of statistics less than the critical value. For Fig. 3 each point for the demographic method represents 80,000 simulations, 40,000 each for the null and alternate cases. Each line-transect point represents 20,000 simulations. The demographic method has four times the number of line-transect simulations because density does not affect power for the demographic technique and therefore 20,000 simulations were accumulated for each of four densities used for line-transect estimates.

As with the vaquita, the simulations are intentionally simplistic and dependent on assumptions about capture rate, sightability, etc. The exercise is not intended as a management answer but is presented to demonstrate techniques useful for evaluation of experimental design. The quality of the evaluation can only be as good as the quality of the preliminary data used in the assessment.

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# An immunochemical approach to quantifying predation by euphausiids on the early stages of anchovy

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ABSTRACT: Off southern California (USA), euphausiid crustaceans appear to be significant predators on the early stages of northern anchovy *Engraulis mordax*. Between 47 and 78 % of the natural mortality of northern anchovy eggs and yolk-sac larvae can be explained by euphausiid predation. The incidence of predation was determined from direct evidence provided by an immunochemical technique that detects anchovy remains in individual euphausiids. Rates of predation were determined from euphausiid feeding rates and digestion rates. The impact on the anchovy population was estimated by quantifying predator abundance by species, estimating predator and prey co-occurrence considering the diel migratory patterns of the predator, determining the number of prey removed $d^{-1}$, and generating natural mortality rates for the anchovy. Euphausiids ate 2.8 % of the anchovy population $d^{-1}$ in the nearshore area and 1.7 % $d^{-1}$ in the offshore area.

## INTRODUCTION

Predation may be a major cause of larval fish mortality in the sea, yet the evidence is not conclusive because methods to assess mortality due to predation have been difficult to develop (Hunter 1984, Sissenwine 1984, Bailey & Houde 1989). Clearly, to discern predator-prey relationships, the predators need to be identified. Direct observation of stomach contents identified planktivorous fish as important predators of fish eggs and larvae (Hunter 1984, Brownell 1985, Dann et al. 1985, Alheit 1987). Likewise, visual analyses of the gastric cavities of gelatinous zooplankters revealed that they can be significant predators on the early stages of fishes (Moller 1984, Purcell 1985, 1989, 1990). Yet predator-prey relationships remain obscure in many situations where predator gut contents cannot be identified through visual analyses.

Direct evidence of predation by carnivorous crustaceans that macerate their prey is limited. In the field, only a few studies report larval fish remains in crustacean guts (Bailey & Yen 1983, Alvariño 1985, Yamashita et al. 1985, Yen 1987) despite the array of crustacean predators identified in the laboratory (Hunter 1984, Bailey & Houde 1989).

Crustacean predators of fish eggs and larvae in the sea need to be identified, and their predation rates need to be quantified. Serological methods that raise antibodies against the target prey successfully detected predation by invertebrates (Boreham & Ohiagu 1978, Feller et al. 1979, Theilacker et al. 1986), and these methods, which yield information on incidence only, can be quantified with additional information (Calver 1984, Sunderland 1988, Theilacker 1988). Recently, Theilacker et al. (1986) developed antibodies to the yolk protein of the northern anchovy *Engraulis mordax*, detected the yolk protein in the gut of a euphausiid crustacean *Euphausia pacifica*, and estimated predation rates at a limited field site (Theilacker 1988).

Here we evaluate, spatially and temporally, northern anchovy egg and larval mortality due to predation by the euphausiid assemblage commonly found in the California Current. We collected anchovy eggs and larvae and euphausiids during 2 California Cooperative Oceanic Fisheries Investigations (CalCOFI) sur-

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veys. CalCOFI has been making seasonal measurements of the physical, chemical and biological characteristics of the California Current for more than 40 yr. CalCOFI cruises encompass the entire anchovy population during the peak of spawning. We analyzed the standardized plankton collections to estimate prey and predator abundance and applied an immunoassay, ELISPOT enzyme-linked immunospot assay, to identify the predators. We used this information to quantify predation rates. The predator net collected adult euphausiids only for the immunoassay. But because it is common for abundance of juvenile (6 to 11 mm) euphausiids to be an order of magnitude higher than adults (>11 mm) (Brinton & Wyllie 1976), we included both size classes to estimate the impact of the euphausiid assemblage on the anchovy population. Ignoring the smaller size class would have underestimated the predation impact.

## METHODS

**Field collections.** Field collections were made on 2 CalCOFI cruises: one in November 1986, prior to peak spawning of northern anchovy, aboard the RV 'New Horizon' and one in March 1987, during peak anchovy spawning, aboard the NOAA vessel 'David Starr Jordan'. We considered the November collections to be a control set. At each station (Fig. 1), euphausiids and anchovy eggs and larvae were collected with standard double oblique plankton tows to 210 m using a Bongo net. Additionally, for the mortality estimates, anchovy eggs and larvae were collected with a CalVET (or PAIROVET) net lowered to a depth of 70 m. Both Bongo and CalVET nets are paired cylindrical-conical nets. The Bongo net frame has 505 µm mesh nets on both sides and the CalVET has 150 and 333 µm mesh nets (Smith & Richardson 1977, Smith et al. 1985). It was shown that there was no extrusion of eggs or larvae through the 150 µm mesh (Lo 1983). The samples were preserved in 5 % buffered formaldehyde.

Non-quantitative, oblique hauls to 50 m were taken to collect euphausiids intended for immunoassays whenever the ship was on station (Fig. 1) between 22:00 and 02:00 h. The depth and time of haul were chosen because many euphausiids migrate toward the sea surface at night (Brinton 1967) where they co-occur with eggs and yolk-sac larvae of northern anchovy which inhabit the upper 50 m of the sea (Ahlstrom 1959). Additionally, feeding activity for *Euphausia pacifica* is maximal after sunset and during most of the night when they have moved into the surface layers (Willason & Cox 1987). Euphausiids were collected using a black, 2 mm mesh Bongo net fitted with a plastic cod end. The dark net color should have decreased predator avoidance, and the large mesh should have allowed the prey to pass through the net, precluding potential biases caused by euphausiids feeding in the net (Nicol 1984). The plastic cod end was used to assure the retrieval of euphausiids in good condition. The large-mesh net selected for larger individuals.

Euphausiids were carefully transferred into buckets of surface seawater, 14 to 15 °C. (Ship's seawater was avoided, as it is often contaminated with metal ions.) Actively swimming euphausiids were selected, blotted quickly to remove excess seawater, and placed individually into 1.5 ml plastic tubes that were set in crushed ice. The sort-

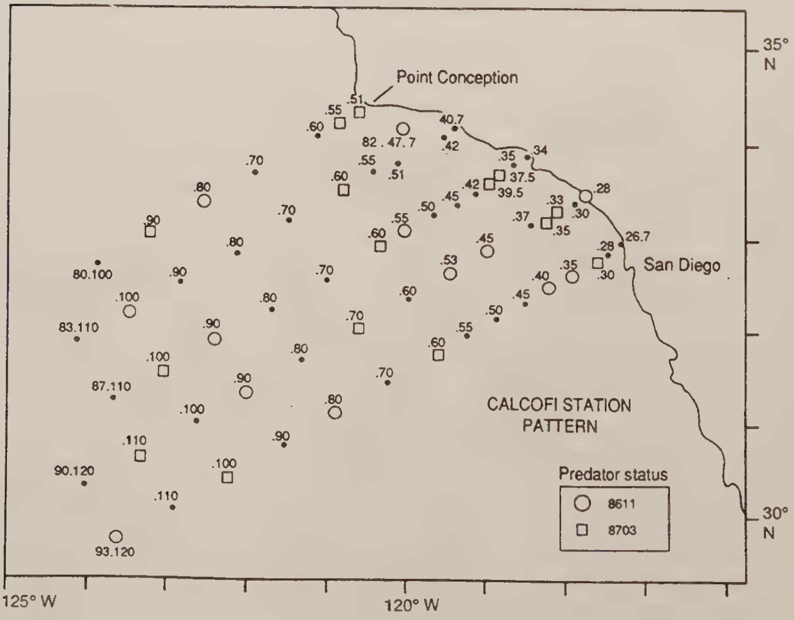


Fig. 1. Station pattern sampled by California Cooperative Oceanic Fisheries Investigations. Stations where separate collections were made for predators are indicated for November 1986 (CalCOFI Cruise 8611) and March 1987 (CalCOFI Cruise 8703)

ing process took about 1 min $ind^{-1}$ from bucket to cooled tube; after 10 min, groups of tubes were frozen at −80 °C.

**Euphausiid abundance.** In the laboratory, all preserved euphausiids were identified to the species level. These included the 6 most common species which were used in the immunological analyses and 10 additional species which were present and also considered to be possible predators. Subsampling and counting procedures are described in Brinton (1976). All specimens ≥6 mm were enumerated in 2 size groups, (6 to 11 mm, >11 mm), then their abundance was standardized to numbers under 10 $m^2$ of water using the standard haul factor (Smith & Richardson 1977). Earlier laboratory experiments with *Euphausia pacifica* showed that feeding rates differed between these 2 size groups (Theilacker & Lasker 1974); euphausiids <11 mm preyed on anchovy eggs and larvae at about one-third the rate of the larger size group.

The stations were divided into 2 categories for analysis. Category 1 included stations with a high euphausiid predation incidence, as determined by the immunoassay, and the other category included stations with a low predation incidence. Any station with predation incidence equal to or greater than the overall average was considered Category 1. Eleven stations from the March cruise were used in the analysis. Offshore stations (Stn numbers greater than 70) were excluded because they are beyond the geographic distribution of anchovy eggs and few yolk-sac larvae were found offshore in past surveys. An analysis of variance procedure was used to compare abundance data of euphausiids >11 mm between the November and March cruises after the total abundance >11 mm from each station was logarithm transformed.

**Prey abundance and mortality rates.** Anchovy eggs were counted, staged, and ages were assigned according to developmental rates (Lo 1985, Moser & Ahlstrom 1985). Then eggs were grouped by half-day categories. Anchovy larvae were counted and measured. Stations used to determine prey abundance were the same stations used in euphausiid collections. Both eggs and yolk-sac larvae were used in the calculation of prey abundance. Standard length of net-collected and preserved yolk-sac larvae is ≤2.5 mm.

Age-specific abundance of anchovy eggs collected from CalVET net tows and size-specific abundance of larvae <9 mm from Bongo net tows were used in computing mortality rates. All stations occupied during the March 1987 cruise were used in this analysis. Preserved larval standard length was converted to live size (Theilacker 1980) and the age was estimated from a temperature-dependent Gompertz age-length growth curve (Methot & Hewitt 1980, Lo 1983). The larval abundance data were adjusted to conform to the following standard conditions: no extrusion (Lo 1983) and a constant water volume filtered per unit depth (Smith & Richardson 1977).

The abundance of larvae in each 1 mm length group was converted to daily production according to the following equation, assuming a steady state. For each station:

$$P_L = \frac{x\,(SHF/10)\,(0.05)}{(R_L)\,(\%\,sort)\,(dr_L)\,(av_L)} \qquad (1)$$

where $P_L$ = daily yolk-sac larval production per 0.05 $m^2$ at average age 5 d from fertilization (<2.75mm); $x$ = no. of 2.5 mm larvae; $SHF$ = standard haul factor, a factor used to convert catch of larvae to the no. of larvae under 10 $m^2$ water (Smith & Richardson 1977); 0.05 ($m^2$) = sea surface area covered by the CalVET net; $R_L$ = retention rate for length $L$ (mm) anchovy larvae (Lo 1983); *% sort* = percent of sample sorted by tow; $dr_L$ (d) = average duration for each 1 mm length interval from 2.5 to 8.75 mm; and $av_L$ = the proportion of larvae that did not avoid the net.

Larval length was converted to age according to the procedures described in Lo (1985, 1986). The decrease in the daily abundance of eggs and larvae with age was considered to be their morality. A single-equation model was chosen to describe anchovy egg and larval mortality (Lo 1986):

$$P_t = P_o e^{-zx_1}\,(x_2/U)^{-\beta}, \qquad (2)$$

where $P_t$ = daily egg or larval production per 0.05 $m^2$ at age $t$ (d); $P_0$ = daily egg production at age 0; $z$ = daily instantaneous mortality rate for eggs and yolk-sac larvae; $x_1$ indexes eggs and larvae younger than age $U$ days, $x_1 = t$ for $t < U$, $x_1 = U$ for $t > U$; $x_2$ indexes larvae older than age $U$ days, $x_2 = U$ for $t < U$, $x_2 = t$ for $t > U$; $U$ = age when the form of instantaneous mortality rate changes; $\beta$ = coefficient for the instantaneous mortality rate for larvae where the daily instantaneous mortality rate = $\beta/t$, $t > U$; and $t$ = age (d).

Mortality rates of anchovy eggs and yolk-sac larvae were initially computed for the 2 high- and low-predation categories. Because of the few stations in each category (6 and 5 stations respectively), we could not detect a difference in total mortality between these 2 categories. In order to obtain a more precise and accurate overall mortality estimate, we used the abundance data for anchovy eggs and larvae (<10 mm) from the entire March cruise.

**Immunoassay.** Aboard ship, a subsample (usually 6 to 10) of each night's euphausiid collection stored at −80 °C was assayed the following day. After the cruise, additional euphausiids were assayed at the Southwest Fisheries Science Center (SWFSC). Details of the immunoassay, a solid-phase enzyme-linked immunospot assay (ELISPOT) are given in Theilacker et al. (1986).

Rabbits were immunized with anchovy yolk protein (the antigen) to prepare the primary, polyclonal antibody. Polyclonal antibodies were used to increase the likelihood of antibody binding to prey proteins that are partially degraded due to euphausiid proteolytic activity.

Only euphausiids >11 mm were used in the assay. The stomach, hepatopancreas and hindgut were dissected out from the body and placed into 10 µl of extraction buffer. Tissues were teased apart, and the extract was dotted onto 0.45 µm pore nitrocellulose paper. The euphausiid gut contents on the nitrocellulose paper was reacted with the primary antibody. If the unknown gut contents contained anchovy yolk protein, it formed a complex with the primary antibody. The resulting antigen-antibody complex was treated with a secondary antibody which had been tagged with the enzyme alkaline phosphatase. The immobilized complex of antigen, primary antibody and secondary antibody on the nitrocellulose paper was visualized with a histochemical phosphatase stain; positive phosphatase activity produced a blue-black color (Theilacker et al. 1986).

In the ELISPOT, the color intensity of the reaction is directly related to the concentration of antigen (Ohman et al. 1991). However, in this situation, the concentration of antigen (yolk) did not correspond to the number of eggs or yolk-sac larvae eaten by the predator. The concentration of yolk ind.$^{-1}$ is not a constant because as eggs and larvae develop, they utilize yolk and the quantity of yolk ind.$^{-1}$ decreases. Thus, in our application, the immunoassay determines only the presence of yolk protein and not the number of eggs or larvae in the predator's gut.

**Gut residence time and detection time.** To estimate daily consumption by the euphausiid assemblage, information on the persistence of yolk protein in the guts of actively feeding individuals at *in situ* temperatures is required. The length of time a meal can be detected in a predator's gut using an immunoassay was designated the 'detection time' (Calver 1984, Sunderland 1988). In the SWFSC aquarium, we fed anchovy eggs to live *Euphausia pacifica* >11 mm collected on the March cruise. In our tests, 20 eggs were fed to individual euphausiids in 500 ml filtered seawater at 14°C. Because earlier experiments showed that *E. pacifica* ate an average of 1 egg in 2 h, the feeding treatment lasted 2 h. The actual time of ingestion was unknown. After 1 or 2 eggs were eaten (determined by counting the remaining eggs), we either immediately froze the euphausiid for the 0-time sample or subsequently fed it algae (non-antibody reactive) and sampled at 30 or 60 min intervals for 6 h. Algae was fed because earlier experiments showed that euphausiids retain their gut contents when feeding is interrupted (Lasker 1966, Willason & Cox 1987).

The percent of tested euphausiids exhibiting a positive reaction to anchovy yolk protein was expected to decrease with time. The difference in % positives between 2 points ($t_1$ and $t_2$) provides an estimate of the proportion of euphausiids whose detection time = $t_2$. If the decrease in % positive is linear, the loss rate per unit time is a constant (slope of the line), and the time corresponding to the 50 % positive is the average detection time. We assayed individual euphausiids using the ELISPOT procedure to determine the average detection time for actively foraging *Euphausia pacifica* >11 mm. We ascribed the average detection time to the >11 mm size category of all species analyzed in this study to compute hourly predation rates.

We have no data on detection time for 6 to 11 mm euphausiids. Ross (1982) found that allometric equations best described the relation between *Euphausia pacifica* body weight and rates of ingestion, respiration, excretion, growth and molting, thus revealing that all weight-specific physiological rates decreased with the increasing weight of the euphausiid. Because we could find no values in the literature to allow for a better assumption, we assumed that the fractional difference in the rate of digestion between 6 to 11 mm euphausiids and >11 mm euphausiids was similar to the fractional difference in feeding rate. Thus, we inferred that the loss rate for yolk protein in 6 to 11 mm euphausiid guts was one-third the loss rate for >11 mm individuals, and we divided the slope of the equation describing *E. pacifica* gut residence time by 3 to estimate the average detection time for the 6 to 11 mm euphausiid assemblage.

**Predation rate.** Daily euphausiid predation was estimated by considering the fraction of the euphausiid population by species that migrate into the depths inhabited by anchovy and the duration that they co-occur in the upper waters. Then the abundance of each euphausiid species by size was multiplied by the species-specific daily ingestion.

Among the euphausiids we sampled, vertical distribution is best known for *Euphausia pacifica*. *E. pacifica* has a daily depth range of 0 to 600 m. Juveniles and adults occupy a daytime depth of 300 to 600 m (Brinton & Wyllie 1976), but reach the upper 50 m at night (Brinton 1967). Brinton (1976) determined that 87 % of *E. pacifica* >6 mm reached the upper 50 m at night. Night was considered 1 h after sunset to 1 h before sunrise; total duration was ca 10 h in March. Thus to calculate predation rate we multiplied the total number of *E. pacifica* under 10 m$^2$ by 0.87. Abundances of the other euphausiids present in the study were similarly adjusted (Table 1).

Species-specific daily ingestion was determined by considering the results of the immunoassay. Because the immunoassay only determined the presence or

Table 1. Day and night vertical range of euphausiid species[a]

| Species | Vertical range | % Population reaching upper 50 m at night | |
|---|---|---|---|
| | | 6–11 mm | >11.5 mm |
| *Euphausia pacifica* | 0–600 m | 87 | 87 |
| *E. gibboides*[b] | 0–600 m | 87 | 87 |
| *E. eximia* | 0–600 m | 87 | 87 |
| *E. recurva* | 0–600 m | 87 | 87 |
| *E. mutica* | 0–600 m | 87 | 87 |
| *E. hemigibba* | 0–600 m | 87 | 87 |
| *Nematoscelis difficilis* | Thermocline to ca 300–600 m | 70 | 40 |
| *N. atlantica* | Thermocline to ca 300–600 m | 70 | 40 |
| *N. tenella* | Thermocline to ca 300–600 m | 70 | 40 |
| *Thysanoessa gregaria* | 0–150 m[c] | 60 | 60 |
| *T. spinifera* | 0–100 m[c] | 87 | 87 |
| *Thysanopoda astylata* | 0–600 m | 87 | 87 |
| *Stylocherion carinatum* | 0–150 m | 87 | 87 |
| *S. affine* | 0–200 m[c] | 87 | 87 |
| *Nictiphanes simplex* | 0–150 m | 87 | 87 |

[a] Data taken from Brinton (1962, 1967)

[b] Adults are >15 mm; they do not usually reach the upper 50 m at night

[c] Day and night depth

absence of yolk protein in euphausiid guts, a Poisson distribution was used to describe the mean no. of prey ingested over an interval of time defined by the duration of gut passage, or the detection time. This distribution assumes that ingestion events were independent and randomly distributed over each time interval. Accordingly, the frequency of negative assays can be related to the number of ingestion events by

$$P(x=0) = e^{-\mu} \qquad (3)$$

where $P(x=0)$ = the probability of no anchovy being eaten (negative immunoassays) and $\mu$ = mean no. of prey ingested per time interval. That is, we equated the relative frequency of zero predation to the exp(−mean) and solved for the mean no. of eggs and yolk-sac larvae eaten by 1 euphausiid. The mean number eaten $h^{-1}$ was estimated by dividing by the laboratory-determined detection time. Ingestion by 6 to 11 mm euphausiids was assumed to be the same as *Euphausia pacifica* of that size and was multiplied by 0.3 to account for their slower feeding rate (Theilacker & Lasker 1974, Ross 1982). Detection time for the 6 to 11 mm group was adjusted as discussed above.

Here a negative assay provides more information than a positive one. A negative assay indicates that the euphausiid predator has not eaten during the measured detection time. A positive assay indicates that the euphausiid has eaten 1 or more prey; there is no temporal information.

To estimate the impact of the euphausiid population preying on the anchovy population, we compared the loss of anchovy with the total natural egg and larval mortality that was determined independently.

## RESULTS

### Field collections

On the November cruise in 1986, plankton collections were taken at 58 stations. At 13 stations, tows for invertebrate predators were also made (Fig. 1). Only 1 of the predator collections was taken inshore where some anchovy spawning had occurred (Fig. 2a).

On the March cruise in 1987, plankton collections were taken at 57 stations. Fifteen invertebrate tows were taken (Fig. 1), and 10 of them corresponded to areas where anchovy eggs and yolk-sac larvae were collected. In 1987, anchovy spawning was moderate in the Southern California Bight (Fig. 2b).

### Euphausiid abundance

The mean abundance of adult euphausiids >11.0 mm, all species combined, was similar between the November (346.5 ind. per 10 $m^2$) and March (287.9 ind. per 10 $m^2$) cruises ($F = 0.33$; df = 1,23; $p = 0.57$; $F$-test computed on log-transformed data). The abundance under 10 $m^2$ at 12 stations in November ($n = 12$) ranged from 18 to 1074 adults, and in March ($n = 13$) abundance ranged from 41 to 1352 adults. The high-abundance, nearshore (<60 mile) stations were dominated by *Euphausia pacifica* and *Nematoscelis difficilis* in November and March (Tables 2 & 3).

Five euphausiid species dominated the assemblage in March; these species were analyzed for evidence of predation and their abundance is detailed here together with information on depth distribution (Table 1) and relative abundance (Brinton 1967, Brinton & Wyllie 1976). A sixth euphausiid species, *Nyctiphanes simplex*, was analyzed for 1 station only (87.39.5; Table 3).

*Euphausia pacifica*, usually the most common species in the southern California area, was present at 9 of the 10 stations used in the predation analysis for the March cruise and was dominant at 5 of the 10 stations.

*Nematoscelis difficilis* is usually second in abundance among the euphausiids in the southern California area. It migrates through a vertical range of about 300 m. The 2 size groups of *N. difficilis* were

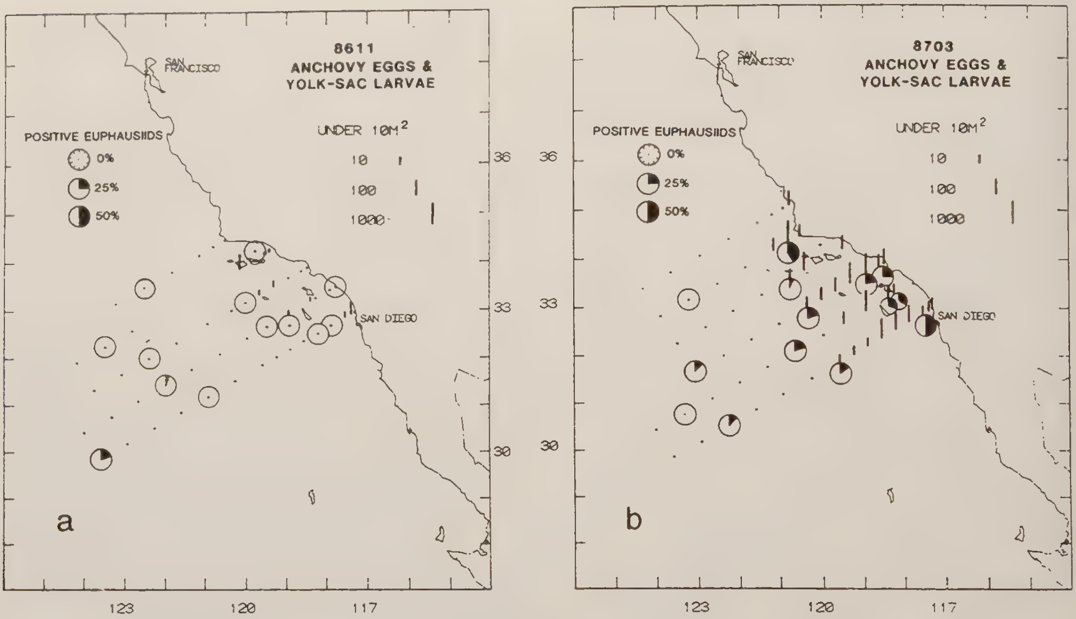


Fig. 2. *Engraulis mordax*. Distribution of positive euphausiid predators, expressed as % positive, superimposed on northern anchovy egg and yolk-sac larval abundance for (a) November 1986 and (b) March 1987. Anchovy numbers adjusted to equal the average abundance under 10 $m^2$ of sea surface

dominant at Stns 87.35 and 93.30 and present at all 10 stations.

*Euphausia gibboides* migrates from a depth of 300 to 500 m in the daytime to the thermocline at night. It was present at 9 of the 10 stations in the study area. Like *Euphausia recurva*, it occurred more offshore than *E. pacifica*, but their distribution overlapped. The highest abundance was at Stn 93.60 with both size groups equal in number. *E. gibboides* adults would not be expected to reach the upper 50 m at night unless the thermocline was particularly shallow, therefore individuals >15.5 mm were not used in the predation estimate.

*Euphausia eximia* was present in 5 of the 10 stations in this study, with its highest abundance at Stn 83.60. All developmental stages of *E. eximia* are concentrated in the surface layer at night.

*Euphausia recurva* migrates from 300–600 m to 0–100 m at night. It was present at 6 of the 10 stations in this study, reaching its highest abundance at Stn 93.60 with a total of 425 ind. per 10 $m^2$ for the >11.5 mm group.

*Nyctiphanes simplex* migrates from 150 m to the surface at night. It was present at 8 of the 10 study stations, and its highest abundances were at Stns 93.30 and 87.39.5.

### Prey abundance and mortality rate

The presence of anchovy prey was minimal in November and abundant in March, with most of the spawning occurring in the Southern California Bight (Fig. 2a, b). In November, anchovy eggs were found at only 1 predator station (36 eggs per 10 $m^2$ at Stn 90.45), whereas in March, abundant eggs and yolk-sac larvae were collected at the nearshore predator stations (Table 4).

Mortality rates for the March cruise were determined using Eq. 2, assuming that eggs and yolk-sac larvae (younger than 5 d) follow an exponential decay ($z = 0.036$, SE = 0.036) and older larvae follow a Perato-type of instantaneous mortality ($\beta = 1.989$, SE = 0.213) (Table 5). $P_0 = 4.13$ eggs per 0.05 $m^2$ (SE = 0.67) for the entire survey area. The *z*-value of 0.036 was later used as the daily mortality rate for both high- and low-predation categories described in the 'Methods' section.

### Euphausiid predation

On the November cruise, only 1 euphausiid collection station (90.45) was taken near shore where there was some anchovy spawning (Fig. 2a). In all, 119 eu-

Table 2. Mean abundance of the dominant euphausiid species under 10 m$^2$ of sea surface taken at stations where predator collections were made in November 1986. 95 % confidence intervals obtained from log$_{10}$ transformation are in parentheses

| Cruise 8611 | Size | | | | Species[a] | | | |
|---|---|---|---|---|---|---|---|---|
| Stn | (mm) | *Ep* | *Er* | *Eg* | *Ex* | *Nd* | Other | Total |
| 80. 80 | 6–11 | 1201 | 120 | 0 | 0 | 529 | 415 | 2265 |
| | >11 | 10 | 71 | 30 | 0 | 30 | 0 | 141 |
| 83. 100 | 6–11 | 3278 | 41 | 20 | 0 | 902 | 798 | 5039 |
| | >11 | 20 | 20 | 20 | 0 | 102 | 0 | 162 |
| 87. 55 | 6–11 | 1227 | 0 | 21 | 0 | 1355 | 297 | 2900 |
| | >11 | 0 | 0 | 22 | 22 | 171 | 0 | 215 |
| 90 | 6–11 | 292 | 136 | 49 | 0 | 970 | 342 | 1789 |
| | >11 | 0 | 10 | 0 | 0 | 49 | 49 | 108 |
| 90. 28 | 6–11 | 0 | 0 | 0 | 0 | 0 | 198 | 198 |
| | >11 | 0 | 0 | 0 | 0 | 0 | 18 | 18 |
| 45 | 6–11 | 1033 | 0 | 32 | 0 | 506 | 295 | 1866 |
| | >11 | 32 | 0 | 11 | 11 | 118 | 0 | 172 |
| 53 | 6–11 | 944 | 22 | 0 | 22 | 630 | 538 | 2156 |
| | >11 | 245 | 0 | 22 | 66 | 741 | 0 | 1074 |
| 90 | 6–11 | 30 | 80 | 10 | 0 | 490 | 712 | 1272 |
| | >11 | 0 | 30 | 10 | 0 | 50 | 0 | 90 |
| 93. 35 | 6–11 | 280 | 0 | 0 | 0 | 992 | 520 | 1792 |
| | >11 | 20 | 0 | 10 | 50 | 682 | 0 | 762 |
| 40 | 6–11 | 902 | 50 | 0 | 40 | 409 | 970 | 2371 |
| | >11 | 122 | 10 | 51 | 10 | 336 | 20 | 549 |
| 80 | 6–11 | 538 | 33 | 22 | 22 | 314 | 707 | 1636 |
| | >11 | 33 | 0 | 11 | 11 | 201 | 0 | 256 |
| 120 | 6–11 | 0 | 83 | 0 | 0 | 0 | 478 | 561 |
| | >11 | 0 | 20 | 10 | 0 | 0 | 581 | 611 |
| Mean: | 6–11 mm | 1987.1<br>(929–2671) | | | | | | |
| | >11 mm | 346.5<br>(106–441) | | | | | | |

[a] *Ep* = *Euphausia pacifica*; *Er* = *E. recurva*; *Eg* = *E. gibboides*; *Ex* = *E. eximia*; *Nd* = *Nematoscelis difficilis*; Other = *E. hemigibba*, *E. mutica*, *N. atlantica*, *N. tenella*, *Nyctiphanes simplex* (*Ns*), *Thysanoessa gregaria*, *T. spinifera*, *Stylocherion affine*, *S. carinatum*, *S. suhmi*, *Thysanopoda astylata*

phausiids were assayed and 2 individuals tested positive for anchovy remains. The 2 positive-reactive euphausiids, both *Euphausia gibboides*, were collected at 2 stations 250 to 350 mile offshore where no eggs or larvae were collected (Fig. 2a).

On the March cruise, predator samples were taken at 10 stations where anchovy eggs and yolk-sac larvae were collected. Between 9 and 50 % of the predatory euphausiids at these stations tested positive (Table 6). In all, 67 or 24 % of the 283 euphausiids assayed tested positive for anchovy yolk protein. Although the relation between percent positive euphausiids and prey abundance was variable at low prey levels, the number of euphausiids eating anchovy seemed to increase rapidly with a small increase in prey abundance (Fig. 3). Maximum percent feeding appeared to be above 1000 prey under 10 m$^2$. Again, as in the November cruise, a few positive-reactive euphausiids (*Euphausia recurva*) were taken from offshore stations outside the anchovy spawning area (Table 6, Fig. 2b).

## Gut residence time and detection time

Results from the digestion experiments showed that yolk protein, consumed by eating 1 or 2 anchovy eggs, could not be detected in the guts of actively foraging euphausiids after 6 h (Fig. 4). The decrease in the percentage of positive euphausiids appeared to be linear with time; an exponential description of the data was

Table 3. Abundance of the dominant euphausiid species under 10 m$^2$ of sea surface taken at stations where predator collections were made in March 1987. 95 % confidence intervals obtained from $\log_{10}$ transformation are in parentheses. Species abbreviations as in Table 2

| Cruise 8703 | Size | Species | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Stn | (mm) | *Ep* | *Er* | *Eg* | *Ex* | *Nd* | Other | Total |
| 80. 55 | 6–11 | 997 | 62 | 10 | 0 | 0 | 82 | 1151 |
| | >11 | 1248 | 0 | 0 | 0 | 104 | 0 | 1352 |
| 90 | 6–11 | 55 | 93 | 0 | 0 | 185 | 485 | 818 |
| | >11 | 0 | 61 | 0 | 0 | 20 | 20 | 101 |
| 83. 60 | 6–11 | 2367 | 216 | 20 | 157 | 512 | 855 | 4127 |
| | >11 | 124 | 0 | 10 | 10 | 59 | 0 | 203 |
| 87. 37.5 | 6–11 | 234 | 0 | 11 | 0 | 87 | 43 | 375 |
| | >11 | 266 | 0 | 11 | 0 | 535 | 0 | 812 |
| 39.5 | 6–11 | 146 | 10 | 10 | 10 | 252 | 817 | 1245 |
| | >11 | 0 | 0 | 0 | 0 | 31 | 10[a] | 41 |
| 60 | 6–11 | 351 | 33 | 11 | 11 | 154 | 308 | 868 |
| | >11 | 111 | 11 | 11 | 0 | 187 | 0 | 320 |
| 100 | 6–11 | 119 | 30 | 0 | 0 | 10 | 590 | 749 |
| | >11 | 0 | 0 | 0 | 0 | 108 | 30 | 138 |
| 90. 33 | | | | Non-quantitative | | | | |
| 35 | 6–11 | 85 | 0 | 11 | 0 | 227 | 65 | 388 |
| | >11 | 202 | 0 | 0 | 0 | 0 | 11 | 213 |
| 70 | 6–11 | 32 | 39 | 19 | 0 | 10 | 108 | 208 |
| | >11 | 11 | 29 | 0 | 0 | 0 | 19 | 59 |
| 110 | 6–11 | 0 | 91 | 0 | 0 | 0 | 280 | 371 |
| | >11 | 0 | 20 | 0 | 0 | 0 | 61 | 81 |
| 93. 30 | 6–11 | 102 | 0 | 0 | 11 | 362 | 498 | 973 |
| | >11 | 152 | 0 | 0 | 0 | 34 | 11 | 197 |
| 60 | 6–11 | 0 | 425 | 42 | 74 | 212 | 509 | 1262 |
| | >11 | 0 | 53 | 21 | 11 | 32 | 22 | 139 |
| 100 | 6–11 | 0 | 304 | 0 | 0 | 0 | 497 | 801 |
| | >11 | 0 | 0 | 0 | 0 | 0 | 86 | 86 |
| Mean: | 6–11 mm | 1025.9<br>(378–1576) | | | | | | |
| | >11 mm | 287.9<br>(93–309) | | | | | | |

[a] The >11 mm size class at this station was mainly *Nyctiphanes simplex*

poor. The weighted linear regression predicted a loss rate of about 13 % h$^{-1}$ (slope), a detection time of 7.2 h, and a 50 % probability of complete digestion of the yolk protein after 3.5 h.

## Euphausiid predation rate

To set up a comparative analysis of prey mortality due to euphausiid predation, we used the computed predation incidence (0.237; Table 6) as a guide for grouping the stations into 2 categories: an area of high predation (≥0.24) and an area of low predation (<0.24). Our hypothesis was that more prey will be eaten in the high-predation area. The high-predation category included the following 6 stations: 93.28, 93.30, 90.33, 90.35, 87.37.5, and 80.55. To have a sufficient number of eggs and larvae for the analysis of prey abundance in the high-predation area, we included Stn 93.28, which was very close to Stn 93.30. The low-predation category contained 5 stations: 93.60, 90.70, 87.39.5, 87.60, and 83.60. Stations in the high-predation category were closer to shore than those in the low-predation category (Fig. 1, Tables 4 & 6).

The potential predation impact by the euphausiid population was estimated by considering the abundance and feeding rate of each predatory species quantified in this study. The nearshore euphausiid spe-

Table 4. *Engraulis mordax*. Abundance of northern anchovy eggs and yolk-sac larvae under 10 m$^2$ of sea surface taken in Bongo net tows at stations where predator collections were made in March 1987

| Cruise 8703 Stn | Anchovy eggs | Anchovy yolk-sac larvae |
|---|---|---|
| 80. 51 | 580 | 32 |
| 55 | 39244 | 793 |
| 90 | 0 | 0 |
| 83. 60 | 0 | 256 |
| 87. 37.5 | 1259 | 13833 |
| 39.5 | 24220 | 15487 |
| 60 | 0 | 1568 |
| 100 | 0 | 0 |
| 90. 33 | 877 | 7787 |
| 35 | 1576 | 7200 |
| 70 | 0 | 0 |
| 110 | 0 | 0 |
| 93. 28 | 559 | 7835 |
| 30 | 525 | 145 |
| 60 | 0 | 389 |
| 100 | 0 | 0 |
| Total | 68840 | 55325 |

Table 5. Daily production under 0.05 m$^2$ ($P_t$) of anchovy eggs (E) and larvae at age $t$ from the March 1987 cruise. Eggs are from 40 stations and larvae are from 46 stations. See 'Methods' for $x_1$ and $x_2$. $P_t$ were computed for the entire survey area in Fig. 1. The inverse of *MSE* was used as case weight for a weighted nonlinear regression

| Egg or larvae (mm) | $t$ (d) | $Pt$ | $x_1$ | $x_2$ | *MSE* |
|---|---|---|---|---|---|
| E | 0.38 | 3.945 | 0.38 | 5 | 1.1394 |
| E | 0.83 | 3.262 | 0.83 | 5 | 1.1394 |
| E | 1.39 | 3.909 | 1.39 | 5 | 1.1394 |
| E | 1.85 | 4.320 | 1.85 | 5 | 1.1394 |
| E | 2.40 | 5.590 | 2.40 | 5 | 1.1394 |
| E | 2.80 | 2.800 | 2.80 | 5 | 1.1394 |
| 2.0–3.0 | 4.87 | 3.570 | 5 | 4.87 | 0.049 |
| 3.5–4.0 | 8.54 | 1.595 | 5 | 8.54 | 0.049 |
| 4.5–5.0 | 11.27 | 0.502 | 5 | 11.27 | 0.049 |
| 5.5–6.0 | 13.65 | 0.311 | 5 | 13.65 | 0.049 |
| 6.5–7.0 | 15.88 | 0.236 | 5 | 15.88 | 0.049 |
| 7.5–8.0 | 18.14 | 0.147 | 5 | 18.14 | 0.049 |
| 8.5–9.0 | 20.34 | 0.153 | 5 | 20.34 | 0.049 |

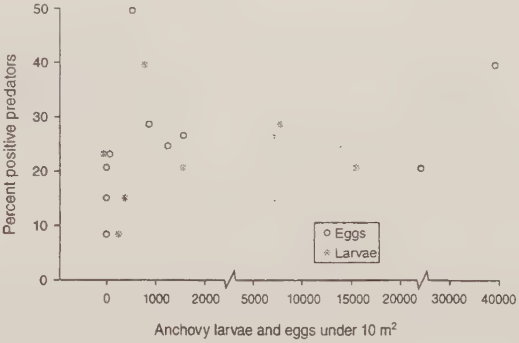
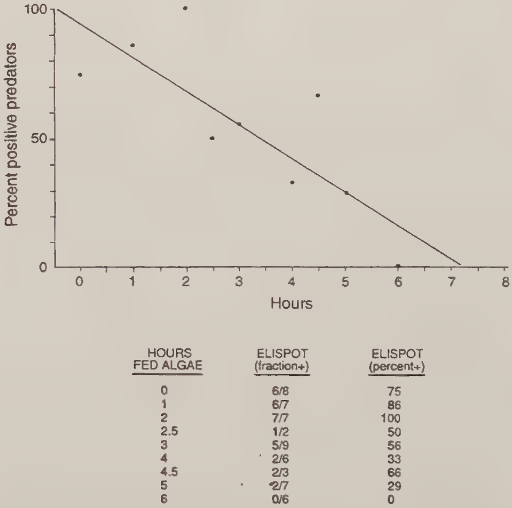


Fig. 3. *Engraulis mordax*. Scatter diagram of abundance of northern anchovy eggs and yolk-sac larvae and the positive-reactive euphausiid predators at concurrent stations in March 1987



| HOURS FED ALGAE | ELISPOT (fraction+) | ELISPOT (percent+) |
|---|---|---|
| 0 | 6/8 | 75 |
| 1 | 6/7 | 86 |
| 2 | 7/7 | 100 |
| 2.5 | 1/2 | 50 |
| 3 | 5/9 | 56 |
| 4 | 2/6 | 33 |
| 4.5 | 2/3 | 66 |
| 5 | 2/7 | 29 |
| 6 | 0/6 | 0 |

Fig. 4. *Euphausia pacifica*, *Engraulis mordax*. Percent of actively foraging *E. pacifica* that have anchovy yolk protein in their guts ($p$, percent positive; no. positive/no. tested) as a function of hours since feeding ($t$, in hours): $p = 94.6 - 12.7\ t$

cies ate 2291 anchovy eggs and yolk-sac larvae d$^{-1}$ per 10 m$^2$, roughly 3 times the number of prey eaten daily by the offshore euphausiids (Table 7). No variances for these estimates were obtained. At these feeding rates, the euphausiid assemblage ate ca 2.8 % of the anchovy population d$^{-1}$ in the nearshore area and 1.7 % d$^{-1}$ in the offshore area (Table 7). This rate of predation accounts for between 47 and 78 % (0.017/0.036 = 0.47; 0.028/0.036 = 0.78) of the anchovy natural mortality (Table 7).

## DISCUSSION

The ELISPOT immunoassay confirmed that predation by euphausiids was a significant source of mortality for the young stages of northern anchovy off California. Anchovy prey may be extremely vulnerable to euphausiids, for the pelagic eggs are spawned

Table 6. Predator stations in March 1987 and frequencies of positive immunoassay reactions (no. positive/no. examined) by species. Species abbreviations as in Table 2

| Cruise 8703 | | | Species | | | | | Positive fraction | Total % positive |
|---|---|---|---|---|---|---|---|---|---|
| Stn | *Ep* | *Er* | *Eg* | *Ex* | *Nd* | *Ns* | Other | | |
| 81. 55 | 8/19 | – | – | – | 0/1 | – | – | 8/20 | 40.0 |
| 90 | 0/1 | 0/2 | – | 0/3 | – | – | – | 0/6 | 0 |
| 83. 60 | 2/20 | – | – | 0/1 | 0/2 | – | – | 2/23 | 8.7 |
| 87. 37.5 | 4/17 | – | 1/2 | – | 0/1 | – | – | 5/20 | 25.0 |
| 39.5 | – | – | – | – | 0/1 | 4/18 | – | 4/19 | 21.1 |
| 60 | 1/7 | 0/1 | 2/4 | 0/1 | 1/5 | – | 0/1 | 4/19 | 21.1 |
| 100 | – | 3/9 | 0/4 | – | 0/7 | – | – | 3/20 | 15.0 |
| 90. 33 | 6/19 | – | – | – | 0/1 | – | 1/4 | 7/24 | 29.2 |
| 35 | 7/25 | – | – | – | – | – | 0/1 | 7/26 | 26.9 |
| 70 | – | 4/15 | 0/2 | – | – | – | – | 4/17 | 23.5 |
| 110 | – | 0/15 | 0/1 | – | – | – | – | 0/16 | 0 |
| 93. 30 | 17/34 | – | – | – | 1/2 | – | – | 18/36 | 50.0 |
| 60 | – | 0/9 | 1/2 | 1/1 | 0/1 | – | – | 2/13 | 15.4 |
| 100 | – | 3/24 | – | – | – | – | – | 3/24 | 12.5 |
| Total | 45/142 | 10/75 | 4/15 | 1/6 | 2/21 | 4/18 | 1/6 | 67/283 | 23.7 |
| % Positive | 31.7 | 13.3 | 26.7 | 16.7 | 9.5 | 22.2 | 16.7 | | |

in a large patch and in an area of high euphausiid concentration at night when the euphausiids rise to the surface. McGurk (1986) has suggested that the patchy distribution of fish eggs and larvae may result in high mortality rates due to predation. During this study between 47 and 78 % of the natural mortality could be ascribed to euphausiid predation. It is reasonable to suggest that predation, and not starvation, was the main source of early mortality since eggs and early larvae are not dependent on exogenous foods.

To analyze our data, we stratified the stations according to predation rate. The population abundance of euphausiids was quantified over the area of co-occurrence with anchovy. Our hypothesis was that more prey will be eaten in areas where the incidence of predation was high. Calculated predation rates that relied on direct evidence of predator gut contents, prey and predator co-occurrence, prey and predator abundance estimates, and predator digestive capacities indicated that the fraction of the anchovy population removed by the euphausiid population was greater nearshore (0.028) than offshore (0.017). Thus euphausiid feeding rate seemed to depend on encounter rate resulting in higher predation nearshore where prey were more abundant. *Euphausia pacifica* dominated the nearshore stations and had the highest (37 %) incidence of predation. An earlier feasibility study had a similar outcome (Theilacker 1988). The incidence of predation by *E. pacifica* detected using ELISPOT was greater (79 %) at a single nearshore station where anchovy densities were higher than at an offshore station (8 %) where anchovy densities were low.

A more meaningful, physiological approach to establishing differences between stations would be to stratify by prey abundance using the prey levels above and below the critical prey level for maximum feeding rate as portrayed by a functional response curve (Peterman & Gatto 1987). Although we do not have sufficient data to determine this level, the general shape of the relation described in Fig. 3 suggests that the maximum percent feeding by euphausiids occurred at prey concentrations of ca 1000 prey per 10 m$^2$. The relation between euphausiid predation and prey abundance appeared to increase rapidly with a small increase in prey level (Fig. 3). In our study, the cutoff used for the high and low predation areas (24 % positive predators) corresponded to what appears to be the critical prey concentration (Fig. 3), lending additional credence to the areas selected for comparison. Additionally, little predation was observed in November 1986 (Fig. 2a) when the maximum prey concentration was 100 per 10 m$^2$.

Although laboratory data on the predatory behavior of some of the assemblage euphausiids is not available, it is clear on grounds of functional morphology as well as experimental evidence and gut content studies, that the relative importance of plant and animal prey differs in euphausiid species (Mauchline 1967). Most euphausiids are omnivorous (Ohman 1984, McClatchie 1985). Stuart (1986) found in the laboratory that adult ($\geq$11 mm) *Euphausia lucens* were able to consume large numbers of anchovy larvae. *E. lucens* also consumes phytoplankton and copepods (Stuart & Pillar 1990). Theilacker & Lasker (1974) showed in laboratory experiments that the median number of yolk-sac anchovy larvae eaten ind.$^{-1}$ d$^{-1}$ by *E. pacifica* ranged from 2 to 17: larval (<6 mm) *E. pacifica* ate 2, juveniles (6 to 11 mm) ate 6, and adults (>11 mm) ate

17. In this study, 6 species tested from the field had eaten anchovy. In the laboratory, euphausiids were capable of consuming enough anchovy prey to meet their daily metabolic requirements (*E. pacifica*, Theilacker & Lasker 1974; *E. lucens*, Stuart 1986). But for *E. pacifica* <11 mm, there appears to be a point of satiation. Offered abundant prey, juvenile *E. pacifica* seldom ate more than 6 larvae $d^{-1}$ (Theilacker & Lasker 1974). Therefore our estimates of 0.1 to 2 anchovy consumed $d^{-1}$ ind.$^{-1}$ seem reasonable considering that they would also be consuming other prey. Likewise, measured phytoplankton ingestion rates of *E. pacifica* studied in the field were low, probably because they were consuming other foods in addition to phytoplankton (Willason & Cox 1987).

Euphausiids are numerically one of the major plank-

Table 7. Comparison between the high- and low-predation stations of euphausiid species-specific feeding rates, the impact of euphausiid predation on the anchovy population, and total anchovy natural mortality rates

| Predator | | Ind. per 10 m$^2$ | No. analyzed | No. not feeding | Freq. of zeros | No. eaten ind.$^{-1}$ h$^{-1a}$ | Fraction co-occurring | No. of anchovy eaten d$^{-1}$ per 10 m$^2$ |
|---|---|---|---|---|---|---|---|---|
| **High predation stations 'inshore'** | | | | | | | | |
| *Euphausia pacifica* | 6–11 mm | 1269 | | | | 0.0125 | 0.87 | 138.05 |
| | >11 mm | 1804 | 114 | 72 | 0.6316 | 0.1313 | 0.87 | 2 060.65 |
| *E. recurva* | 6–11 mm | 62 | | | | | | |
| | >11 mm | 0 | 0 | | | | | |
| *E. giboides* | 6–11 mm | 32 | | | | 0.0189 | 0.87 | 5.25 |
| | 11.5–15 mm | 0 | 2 | 1 | 0.5000 | 0.1980 | 0.87 | 0.00 |
| *E. eximia* | 6–11 mm | 11 | | | | | | |
| | >11 mm | 0 | 0 | | | | | |
| *Nematoscelis difficilis* | 6–11 mm | 816 | | | | 0.0061 | 0.70 | 34.68 |
| | >11 mm | 138 | 5 | 4 | 0.8000 | 0.0638 | 0.40 | 35.19 |
| *Nyctiphanes simplex* | 6–11 mm | 508 | | | | | | |
| | >11 mm | 11 | 0 | | | | | |
| Other | 6–11 mm | 202 | | | | 0.0061 | 0.87 | 10.67 |
| | >11 mm | 22 | 5 | 4 | 0.8000 | 0.0638 | 0.87 | 12.20 |
| Total | 6–11 mm | 2900 | | | | | | |
| | >11 mm | 1975 | 126 | | | | | |
| Total no. of anchovy eaten | | | | | | | | 2 291.45 |
| No. of anchovy eggs & larvae per 10 m$^2$ | | | | | | | | 81 633.18 |
| Fraction of anchovy population eaten d$^{-1}$ | | | | | | | | 0.028 |
| Total mortality, *Z* (SE) | | | | | | | | 0.036 (0.036) |
| **Low predation stations 'offshore'** | | | | | | | | |
| *E. pacifica* | 6–11 mm | 3130 | | | | 0.0032 | 0.87 | 87.27 |
| | >11 mm | 512 | 27 | 24 | 0.8889 | 0.0337 | 0.87 | 149.90 |
| *E. recurva* | 6–11 mm | 723 | | | | 0.0178 | 0.87 | 111.93 |
| | >11 mm | 93 | 25 | 13 | 0.5200 | 0.1868 | 0.87 | 151.17 |
| *E. giboides* | 6–11 mm | 113 | | | | 0.0128 | 0.87 | 12.57 |
| | 11.5–15 mm | 53 | 8 | 5 | 0.6250 | 0.1343 | 0.87 | 61.92 |
| *E. eximia* | 6–11 mm | 252 | | | | 0.0110 | 1.00 | 27.80 |
| | >11 mm | 21 | 3 | 2 | 0.6667 | 0.1158 | 1.00 | 24.33 |
| *N. difficilis* | 6–11 mm | 1675 | | | | 0.0032 | 0.70 | 37.58 |
| | >11 mm | 396 | 9 | 8 | 0.8889 | 0.0337 | 0.40 | 53.31 |
| *N. simplex* | 6–11 mm | 836 | | | | 0.0068 | 0.87 | 49.74 |
| | >11 mm | 10 | 18 | 14 | 0.7778 | 0.0718 | 0.87 | 6.25 |
| Other | 6–11 mm | 1814 | | | | 0.0000 | 0.87 | 0.00 |
| | >11 mm | 41 | 1 | 1 | 1.0000 | 0.0000 | 0.87 | 0.00 |
| Total | 6–11 mm | 8543 | | | | | | |
| | >11 mm | 1126 | 91 | | | | | |
| Total no. of anchovy eaten | | | | | | | | 717.78 |
| No. of anchovy eggs & larvae per 10 m$^2$ | | | | | | | | 41 920.53 |
| Fraction of anchovy population eaten d$^{-1}$ | | | | | | | | 0.017 |
| Total mortality, *Z* (SE) | | | | | | | | 0.036 (0.036) |

[a] Poisson distribution was assumed

tonic organisms in the eastern north Pacific (Boden et al. 1955). They co-occur with the eggs and larvae of pelagic spawning fishes. The euphausiid abundances that we calculated are averages. At times, abundances of euphausiids are extremely high. Surface swarms of *Thysanoessa spinifera* are common events off California during spring and summer (Smith & Adams 1988). There are numerous theories, including congregating to feed, about the mechanisms that cause swarming, but Smith & Adams (1988) argue that it is mainly related to reproduction. Likewise, Endo et al. (1985) concluded that *E. pacifica* in Sendai Bay, Japan, swarmed for reasons other than feeding (e.g. possibly mating). On the other hand, Brown et al. (1979, in McClatchie 1985) note that swarms of *Meganyctiphanes norvegica* in the Bay of Fundy preyed on copepods. Stimuli for swarming are complex and probably vary (Komaki 1967, Antezana et al. 1972). However, the tendency for euphausiids to concentrate near the surface during swarming could contribute importantly to variability in predation mortality of anchovy larvae.

In addition to euphausiids preying on the young stages of fish, other carnivorous invertebrates in the California Current also may eat fish eggs and larvae. The biomass of calanoid copepods appears to be about 3 times that of euphausiids (Isaacs et al. 1969). In laboratory experiments, some predatory copepods can consume as many fish larvae $d^{-1}$ as euphausiids (Hunter 1984, Bailey & Houde 1989); however, unlike euphausiids (Theilacker & Lasker 1974), copepod feeding rate is reduced in the presence of an alternate prey (Lillelund & Lasker 1971, Bailey & Yen 1983). Thus, it is reasonable to expect euphausiids to continue to feed on larvae when they are available.

In the field, gelatinous invertebrates are considered significant predators on both eggs and larvae (Moller 1984, Purcell 1985, 1989, 1990). De Lafontaine & Leggett (1988) consider jellyfish predation to be the primary cause of mortality of larval capelin *Mallotus villosus*. In the California Current, jellyfish are not a significant portion of the plankton assemblage during the anchovy spawning season (Alvariño 1980). Planktivorous fish are abundant in upwelling systems, and they are significant predators of fish eggs (MacCall 1980, Dann et al. 1985, Alheit 1987). Hunter & Kimbrell (1980) estimated that 17.2 % of the population of northern anchovy eggs was removed by cannibalism; the impact on fish larvae is more difficult to assess due to the rapid digestion of the larvae by the fish. In the laboratory, it seems that predatory fishes mainly consume eggs and older, more visible fish larvae, whereas the yolk-sac stages are less vulnerable (Folkvord & Hunter 1986, Pepin 1987, Margulies 1989).

Identifying the major predators of the young stages of fish and measuring and quantifying their impact is a massive undertaking. The immunochemical method offers a powerful approach for identifying potential crustacean predators and elevating the status of a potential predator to a positive one. Currently the ELISPOT immunoassay is being used to study predation by amphipods, mysiids, and euphausiids on the young stages of walleye pollock *Theragra chalcogramma* in the Gulf of Alaska (Bailey et al. in press).

Immunoassay surveys provide an important method to identify factors affecting recruitment processes. Thus, we feel it is essential to comment on the inherent limitations of the immunoassay and on the assumptions we made, and to make recommendations for future studies.

One limitation of our antiserum is that it does not differentiate between predators feeding on eggs or on yolk-sac larvae. Laboratory experiments show that euphausiids and copepods mostly consume yolk-sac larvae, and that they appear to be ineffective predators on eggs (Hunter 1984). A possible reason for this result is that most pelagic eggs float on the surface in static laboratory containers and are unavailable to the predators. In the sea, where mixing occurs above the thermocline, Ahlstrom (1959) has shown that pelagic eggs are well distributed. Additionally in the field, Bailey et al. (unpubl.) have detected walleye pollock egg yolk protein in the guts of predatory invertebrates prior to the period of hatching.

Another limitation that complicates the quantification process is that the immunoassay, as applied in this study, yielded information only on the presence or absence of yolk protein in the predator's gut. Thus, in addition to not differentiating between egg and yolk-sac larvae, it did not distinguish between 1 or more prey having been eaten. Consequently, this approach is appropriate to study predators that have low daily consumption rates. Daily consumption rates measured in the laboratory for copepods, euphausiids, and amphipods range from 1 to 24, albeit at prey densities higher than those that occur in the field (Hunter 1984, Bailey & Houde 1989).

Spurious reactions could occur if the antisera cross-reacts with yolk protein from other fish. Using our antibody preparation, we have obtained cross-reactions with dot blots of yolk from single eggs (ca 60 µg yolk protein dry wt $egg^{-1}$) of sardine *Sardinops sagax* Pacific mackerel *Scomber japonicus* and Pacific herring *Clupea pallasi*. However, we have additional experimental evidence that suggests yolk protein from other fish could not be detected *in vivo*.

We compared equivalent amounts of Pacific mackerel and anchovy yolk protein in an ELISPOT titre test. Side-by-side testing revealed a much reduced reaction for mackerel protein at all protein concentrations and no visible reaction at protein concentrations less than 0.3 µg. Thus, it appears Pacific mackerel yolk proteins have few antigenic sites in common with anchovy protein. Since we rarely find more than 0.3 µg of anchovy yolk protein in euphausiid stomachs, presumably due to the degradation of the yolk protein by euphausiid proteolytic activity (an anchovy yolk-sac larvae contains about 6 µg yolk protein; Theilacker et al. 1986), we assume that mackerel and other fish yolk proteins will behave similarly and that after digestion by euphausiids too few sites will be retained to elicit a visible reaction.

To determine whether cross-reactions occurred in the field samples, we collected and tested predators off California in November before peak anchovy spawning when other fish eggs and larvae were present (Fig. 5). Because most of the euphausiids (117/119, 98.3 %) tested negative, we did not consider cross-reactions to be a problem.

We obtained a few spurious reactions outside the anchovy spawning area. Two *Euphausia gibboides* in November and 6 *E. recurva* in March, collected west of Stn 90 on lines 87 and 93 (Figs. 1, 2a, b), tested positive for anchovy yolk protein. We cannot explain these spurious reactions, but it is in the realm of possibilities that anchovy eggs from the western boundary of the spawning area could be entrained in eddys or filaments and relocated offshore. Fiedler (1986) deduced from satellite imagery and field information that in March of 1985 an eddy entrained and transported anchovy larvae to the same offshore area between lines 87 and 93. This was a recurrent eddy, found in an anomalous location in March 1985. The total time for transport to carry water offshore is not well known, although filament speeds of up to 0.7 m $s^{-1}$ have been documented off central California (Strub et al. 1991). Speeds this strong could transport anchovy embryos offshore where the predators were collected within 6 d, the period that yolk is retained in developing anchovy. Yet the collecting nets sampled no anchovy products in this offshore area. Perhaps euphausiids, which encounter larger spheres and integrate over longer time periods than nets do, are better samplers than nets. In any event, these few curious, positive-reactive euphausiids contributed little to the overall estimate of the predation impact.

We made several assumptions which, if wrong, could modify the outcome. The calculation of the predatory impact of the euphausiid assemblage is sensitive to the functions describing ingestion and gut residence time. Here we used the measured rate for *Euphausia pacifica* gut residence time, and because little was known about this rate for the 5 other species studied, we ascribed the *E. pacifica* rate to them as well. Fifty percent of the euphausiids examined in this study were *E. pacifica*. The assumptions we made were: (1) the 6 to 11 mm size class of the investigated species feeds at the same rate as *E. pacifica* of that size; (2) gut residence time of anchovy yolk protein for the investigated euphausiids >11 mm is the same as for *E. pacifica* >11 mm; and (3) gut residence time for the 6 to 11 mm group is 3 times that of euphausiids >11 mm.

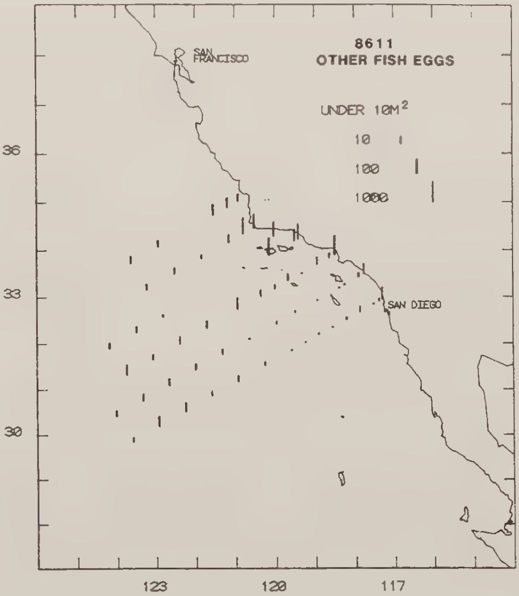


Fig. 5. Abundance of other fish eggs in November 1986. Egg numbers adjusted to equal the average abundance under 10 m$^2$ of sea surface

Willason & Cox (1987) determined the residence time for phytoplankton pigment in the guts of *Euphausia pacifica* >11 mm after feeding them on charcoal particles. They used an exponential model to describe gut clearance. Using their model, we calculated that 3 to 5 % of the initial pigment remained in the euphausiid guts after 3.5 h, the average detection time determined for our experiments. Although they found that some plant pigment still could be measured in the guts for 10 h, we found no detectable yolk protein after 6 h. Thus, their measurements for gut residence time of phytoplankton prey for euphausiids >11 mm differ somewhat from our gut clearance measurements for ichthyoplankton prey. Willason & Cox (1987) did not study the smaller size class, and we could find no values in the literature for euphausiids <11 mm.

Clearly, further studies are needed to substantiate size-specific functions for ingestion and detection time for the primary predator species. An accurate measure of predation for the 6 to 11 mm size group is important. In our study area, the total number of 6 to 11 mm euphausiids at the low-predation stations was about 8 times the number of >11 mm euphausiids. It is common for abundance of 6 to 11 mm euphausiids to be an order of magnitude higher than the >11 mm size class (Brinton & Wyllie 1976).

We believe our results are conservative. Predator abundance may be underestimated due to euphausiids avoiding the collecting net and to their contagious distributions that we discussed earlier. Additionally, we may have overestimated average detection time because 25 % of the individuals tested in the laboratory had completely digested the protein within the 2 h feeding trial (see euphausiids at Hour 0, Fig. 4).

In the future, to resolve the potential cross-reaction dilemma, we suggest testing the gut contents of euphausiids fed in the laboratory on the eggs or larvae of other, co-occurring fishes. Ideally it would be best to dedicate a cruise to this study and to take sufficient samples to confidently estimate mortality rates using only eggs and yolk-sac larvae.

Our study showed that euphausiids are important predators on the early life history stages of anchovy. The impact of the euphausiid population was substantial. Euphausiid crustaceans are ubiquitous in the sea and numerically one of the major planktonic organisms in the eastern north Pacific (Boden et al. 1955) having a great potential to impact all fish populations that spawn pelagic eggs.

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# Composition of the Hawaiian Monk Seal Population at Kure Atoll, 1990[1]

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ABSTRACT: Population recovery–related management actions have been taken to rebuild the endangered Hawaiian monk seal (*Monachus schauinslandi* Matschie) colony at Kure Atoll in the Northwestern Hawaiian Islands since 1981. In 1990, composition of the Kure population was determined by a combination of methods to identify all seals using the atoll. The resident 1990 population included 75 seals, and an increasing trend in the mean annual beach count of seals over the last decade is apparent. Two major changes have occurred in the population since 1985. A shift in the adult sex ratio (males/females), from 2.7:1 to 0.8:1, has developed and appears to be due to both adult male losses and increased recruitment of females. Also, the declining trend in births apparent between 1981 and 1986 has been reversed. These findings suggest cause for optimism for the continued growth of this population.

THE ENDANGERED Hawaiian monk seal (*Monachus schauinslandi* Matschie) uses the beaches of the Northwestern Hawaiian Islands (NWHI) to rest, molt, and give birth. Kure Atoll, the westernmost group of islands in the Hawaiian Archipelago, supports a population of monk seals that was significantly depleted during the 1960s and 1970s (Kenyon and Rice 1959, Rice 1960, Wirtz 1968, Johnson et al. 1982). The decline was attributed to harassment of seals by U.S. Coast Guard Kure loran station personnel, dogs, and vehicles driven on the beaches where the seals gave birth and nursed their pups (Kenyon 1972). By the 1970s, reduced pup survival had become apparent as low numbers of immature seals in the beach counts, a declining number of adults, and decreasing numbers of births each year (Johnson et al. 1982, Gerrodette and Gilmartin 1990).

Recently, several management actions have contributed to a recovering trend in the population. In the late 1970s and continuing through the 1980s, the U.S. Coast Guard personnel at Kure Atoll curtailed their beach activities, and some areas of beach were placed off limits (Gerrodette and Gilmartin 1990). Also, in 1981 the National Marine Fisheries Service (NMFS) initiated the Head Start Project to enhance the survival of female pups at Kure Atoll (Gilmartin et al. 1986, Gerrodette and Gilmartin 1990). Although the Head Start Project successfully increased young female suvivorship, the aged composition and low productivity of this population dictated that additional action was necessary to facilitate recovery. Beginning in 1985, the population was bolstered by an annual addition of two to three yearling females from French Frigate Shoals. These seals were collected as underweight pups and fattened in captivity for up to 10 months before introduction to the Kure population. Together, these management actions have reversed the general declining trend in Kure births and beach counts, and the prognosis for recovery now appears good (Gerrodette and Gilmartin 1990, Henderson and Finnegan 1990). The work presented in this paper is an assessment of the composition of the Kure monk seal population in 1990. Also included is a discussion of the changes that have occurred since 1985, when the last comprehensive assessment of the population, including adult composition, was conducted by Reddy and Griffith (1988).

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## METHODS

Fieldwork to determine the composition of the Hawaiian monk seal population at Kure Atoll was conducted from 7 February to 20 May 1990. Beach counts of seals on all islands in the atoll were conducted three times each week using methods described in Stone (1984). Seals observed on the beaches were classified according to size and sex and individually identified by one or more of the following: (1) uniquely numbered hind flipper tags that had been applied to all weaned pups in the population since 1981 (Gilmartin et al. 1986), (2) distinctive scar patterns that had been photographed and hand drawn onto seal "scar cards" in 1990 and earlier years, and (3) unique bleach marks applied in 1990 to the pelage of seals as described by Stone (1984). The ages of all tagged seals were known from tagging records. Any animal seen for the first time (i.e., had not been previously identified on the basis of tags, scars, or earlier bleach marks) was given a bleach mark and/or its scars were photographed to document its presence at the atoll. Beach counts continued until 11 September, but no new seals were seen after 24 March. Beach counts from April through June in 1990 were compared with counts made in the same months over the last decade because data from this time bracket are available for all years.

In addition to the resident seals using Kure Atoll identified in February–May 1990, eight seals were added by NMFS to the population. On 2 May, two rehabilitated female yearling seals (born and collected at French Frigate Shoals in 1989 and held at Sea Life Park, Oahu, until they gained sufficient weight) were transported to Kure Atoll by U.S. Coast Guard aircraft, as was a third rehabilitated female on 30 May. These three yearlings were maintained in a fenced shoreline enclosure on Green Island, the largest island in the atoll, for 5–7 weeks before release. In addition, five weaned female pups collected at French Frigate Shoals in 1990 were transported by the NOAA ship *Townsend Cromwell* directly to Kure Atoll. These five seals were placed in the fenced shoreline enclosure when they arrived on 26 July. They were fed and maintained in the enclosure along with three female pups born at Kure Atoll in 1990. All eight of these pups were released from the enclosure between 21 August and 15 September 1990.

## RESULTS AND DISCUSSION

The mean beach count of seals between 1 April and 30 July 1990 was 26.0, excluding pups of the year, and 29.5, including pups. The five weaned female pups from French Frigate Shoals that arrived at Kure Atoll in late July are not included in these counts. The mean beach count in 1990 was lower than in 1988 and 1989, but was still consistent with the long-term trend in increasing beach counts observed during the decade since NMFS recovery actions were initiated in 1981 (Figure 1). The mean count for 1991 was 33.1 seals (NMFS, unpublished data), which clearly supports the conclusion that the population is increasing. The reduced mean beach count (as well as births) observed at Kure Atoll in 1990 occurred at all the major monk seal breeding sites that year and was believed to be due to a food stress on the population that affected reproductive rates and hauling patterns (Gilmartin et al. 1991).

The age and sex composition of the population in 1990 comprised all identified seals including pups and yearlings transported to Kure Atoll in 1990 (Table 1). This is compared with the only earlier complete enumeration of the Kure Atoll population, which was performed in 1985 (Reddy and Griffith 1988). The ratio of mature to immature seals was unchanged from 1985 to 1990, but an important change occurred in the sex composition. The number of adult females doubled, and the number of adult males declined, causing a shift in the adult sex ratio (male/female) from 2.7:1 in 1985 to 0.8:1 in 1990. The loss of adult males did not appear to be due to migration to other islands; the decline was probably a result of deaths of old males that were born in the early 1960s. This change in sex ratio was a critical goal of the recovery actions at Kure Atoll because some males in the breeding populations at Laysan and Lisianski islands, which have had highly male-

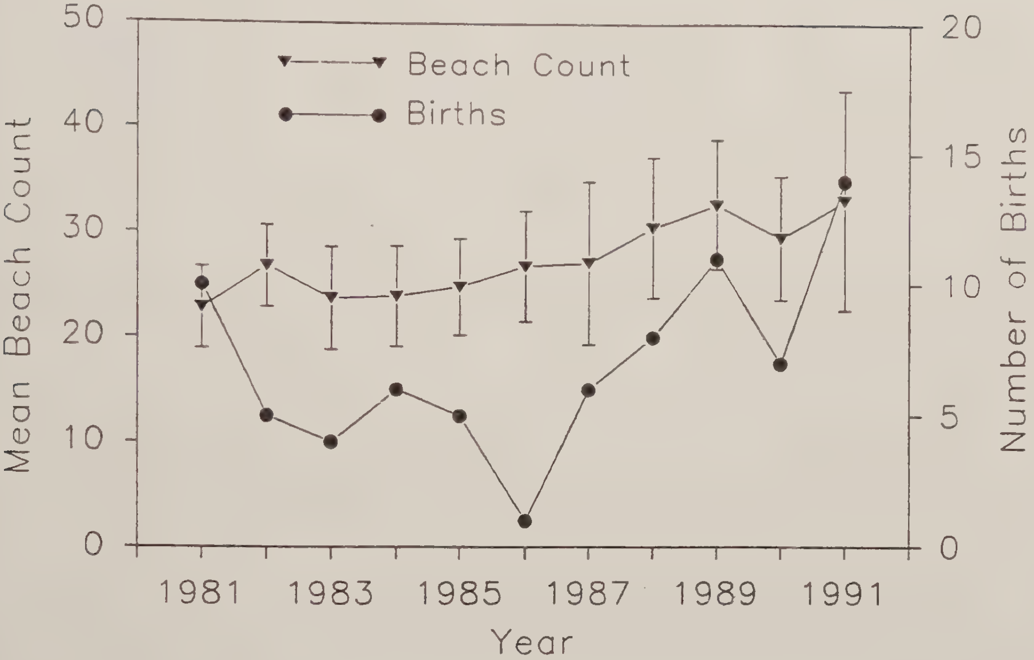

FIGURE 1. Mean beach counts (including pups) and number of births at Kure Atoll, 1981–1991. Bars indicate one standard deviation.

TABLE 1

POPULATION STRUCTURE AT KURE ATOLL FOR 2 YR IN WHICH THE POPULATION WAS ENTIRELY MARKED

| | | NO. OF SEALS | |
|---|---|---|---|
| SEX | SIZE | 1985 | 1990 |
| Female | Adult | 10 | 23 |
| | Immature | 12 | 12 |
| | Pup | 3 | 3 + 5 |
| Male | Adult | 27 | 19 |
| | Immature | 14 | 10 |
| | Pup | 2 | 3 |
| Total females | | 25 | 43 |
| Total males | | 43 | 32 |
| Grand total | | 68 | 75 |
| Adult sex ratio (M : F) | | 2.7 : 1 | 0.8 : 1 |
| Mature : immature ratio | | 1.2 : 1 | 1.3 : 1 |

biased adult sex ratios, exhibit a behavior of mass breeding attacks on adult females that commonly result in severe injuries and death (Hiruki et al. 1993).

The annual number of births also has recovered from the downward trend ending in 1986 (Figure 1). Some of the 1981 "graduates" of the Head Start Project began giving birth in 1987, and since then, births have clearly increased. As expected, an increasing proportion of the births each year were from Head Start and rehabilitated females. The drop in births in 1990 was observed at all of the major monk seal breeding sites in the NWHI and appeared to be a result of a smaller fraction of females giving birth because of a food stress on the population (Gilmartin et al. 1991). This change was transient at Kure Atoll, as the number of 1991 births illustrates.

Over the last decade, successful management has enhanced the recovery of the Kure Atoll population of Hawaiian monk seals. Survival of Kure-born female pups has been increased since 1981, and yearling females have been added to the population annually since 1985. In addition, the population has been bolstered by a one-time addition of five weaned female pups from French Frigate

Shoals, and the amount of disturbance to the population has been decreased by continuing education of resident U.S. Coast Guard personnel. These actions have not only increased the size of the population, but also have dramatically changed its composition. The aged Kure population of the 1970s and early 1980s with a high adult male to female sex ratio was transformed over the last decade into a population composed of a healthy proportion of young seals with an overall sex ratio favoring females. The outlook for the Kure Atoll population of monk seals is optimistic.

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# Estimates of Cetacean Abundance and Distribution in the Eastern Tropical Pacific

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## ABSTRACT

Large-scale research vessel surveys were conducted annually from 1986 through 1990 by the US National Marine Fisheries Service to monitor the abundance of dolphin populations in the eastern tropical Pacific Ocean (ETP). Stratified line-transect surveys with two vessels sampled an area of 19 x $10^6$ km$^2$. Sightings of all cetaceans were recorded, leading to the identification of 29 species. Distribution maps are presented for all species. Data from all five surveys were pooled to give single estimates of abundance in the ETP for 24 stocks of cetaceans representing 19 species or genera. Abundance estimates totaled 9.6 million animals for all dolphin species (subfamilies Delphininae and Steninae), 292,800 for all species in the subfamily Globicephalinae, 45,300 for all species in the family Ziphiidae (beaked whales), 33,881 for all species in the superfamily Physeteroidea, representing 22,666 sperm whales and 11,215 dwarf sperm whales, and 14,431 for two species in the family Balaenopteridae (rorquals), representing 13,023 Bryde's whales and 1,415 blue whales.

KEYWORDS: ETP; ASSESSMENT; SURVEY-SHIP; SMALL CETACEANS – GENERAL; SPOTTED DOLPHIN; STRIPED DOLPHIN; SPINNER DOLPHIN; COMMON DOLPHIN; FRASER'S DOLPHIN; BOTTLENOSE DOLPHIN; RISSO'S DOLPHIN; ROUGH-TOOTHED DOLPHIN; PILOT WHALE; MELON-HEADED WHALE; FALSE KILLER WHALE; PYGMY KILLER WHALE; BEAKED WHALES; CUVIER'S BEAKED WHALE; PYGMY BEAKED WHALE; BLAINVILLE'S BEAKED WHALE; SPERM WHALE; DWARF SPERM WHALE; BRYDE'S WHALE; BLUE WHALE.

## INTRODUCTION

In 1986 the US National Marine Fisheries Service (NMFS) initiated a long-term, large-scale research program to monitor trends in the abundance of dolphin populations in the eastern tropical Pacific (ETP). The program utilized two research vessels annually for 120 days each, from 1986 to 1990, for a total of five surveys. Although the purpose of the surveys was to monitor dolphin abundance, sightings of all cetaceans were recorded. These surveys provided a unique opportunity to describe the abundance of the entire cetacean fauna in the ETP. Here we pool all five years of data to estimate abundance in the eastern tropical Pacific for 24 stocks of cetaceans representing 19 species or genera. A stratified analysis incorporating line-transect methods similar to Wade and Gerrodette (1992) was used.

There are few previous estimates of abundance for most of the species considered here. Polacheck (1987) compared the relative density of eight species of cetacean in the ETP, using encounter rates of cetacean schools with tuna purse-seiners, but did not make abundance estimates. Data from the tuna purse-seiners have also been used to estimate trends in relative abundance for three dolphin species that experience mortality in the fishery, a recent example being Buckland *et al.* (1992). Annual abundance estimates have been made for stocks of four species of dolphins that experience mortality in the fishery (Wade and Gerrodette, 1992), using the same data as in this paper. Abundance estimates for those four species are repeated here, but as single pooled estimates rather than as annual estimates. Estimates are presented for the first time for 15 other species or genera of cetaceans. Additionally, distribution maps for sightings of all 29 species are presented.

## MATERIALS AND METHODS

### Study area and survey methods

The five surveys occurred between late July and early December each year between 1986 and 1990. The surveys were designed to replicate each other as closely as possible, using the same methods, the same vessels and many of the same observers each year. The outside boundary of the study area was described by Au *et al.* (1979). The study area was partitioned into four areas or strata: inshore; middle; west; and south (Fig. 1). The size of each stratum was calculated by Holt and Sexton (1990). The number of ships, the total amount of survey effort needed to achieve a given precision and the allocation of survey effort by stratum were described in Holt *et al.* (1987).

The NOAA research vessels *David Starr Jordan* and *McArthur* traversed randomly placed predetermined tracklines in the ETP for approximately 120 days at sea in each year (Fig. 1). While on duty, two observers searched from directly ahead to abeam of the ship using 25x binoculars while a third searched directly ahead of the ship when not recording data. When a school was initially detected, the observers estimated the angle and radial distance to the school. Angles were read directly to the nearest degree from a scale on the binocular stand, while radial distances were measured by reading calibrated reticles in the binocular eyepiece. Perpendicular distances were calculated as the radial distance multiplied by the sine of the angle, in radians. When possible, cetacean schools were approached to confirm species identification and to make estimates of school size. Dolphin schools more than 5.6km (3 n.miles) from the trackline were not routinely approached. Whale sightings were only approached when

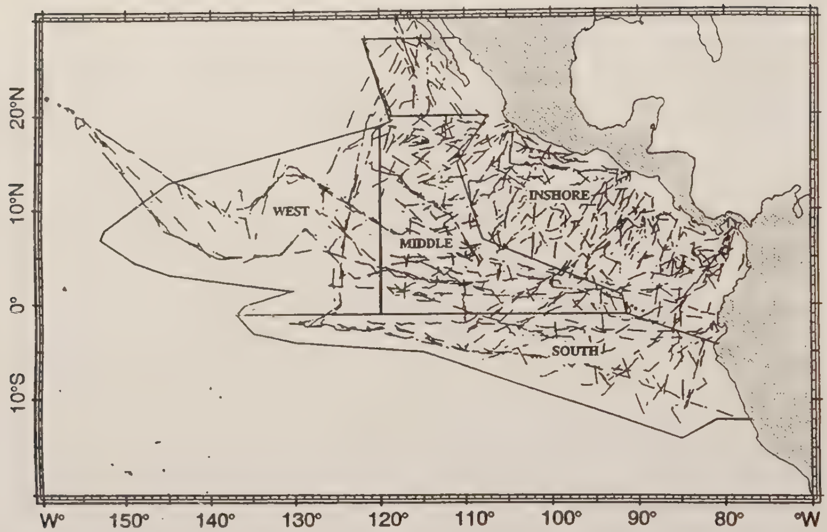

Fig. 1. Study area, strata, and survey tracklines 1986–90 in the eastern tropical Pacific. Solid, continuous lines define outer perimeter of study area and partitions between the 4 strata: inshore, middle, west, and south. Broken lines represent 'on-effort' tracklines of the marine mammal survey.

convenient; consequently, many of these sightings were not identified to species, but to some larger category such as 'rorqual'.

**Data selection**

Legs of effort from Beaufort states 0-5 were used, discarding a small amount of Beaufort 6 effort. Only schools detected within 5.5km (2.97 n.miles) perpendicular distance of the trackline were used (this is lower than the value of 7.4km used by Tobayama *et al.*, 1992). The perpendicular distances were grouped into eleven bins of 0.50km width for the analysis. For each sighting, from one to six observers estimated school size, with the most frequent number being three. Therefore, school size estimates were averaged across observers to obtain the mean of their estimates. Sightings with only a reported minimum estimate of school size were not used in the calculation of mean school size, but were used otherwise, contributing to $n_{jk}$ and the estimation of $f_{jk}(0)$ (see Eq. 1 below).

**Stocks estimated**

The term 'stock' will be used to refer to the category for which an abundance estimate was made. Dolphins from some stocks are killed during tuna purse-seining operations in the ETP. The major populations affected by the fishery are the offshore stocks of spotted dolphins (*Stenella attenuata*) and the eastern and whitebelly stocks of spinner dolphins (*S. longirostris*) (Smith, 1983). A number of other species, including common dolphins (*Delphinus delphis*), striped dolphins (*S. coeruleoalba*), Fraser's dolphins (*Lagenodelphis hosei*), rough-toothed dolphins (*Steno bredanensis*), bottlenose dolphins (*Tursiops truncatus*) and short-finned pilot whales (*Globicephala macrorhynchus*), have also been killed (e.g., Hall and Boyer, 1989).

For the three species of *Stenella* and *Delphinus delphis*, abundance estimates were made for the nine stocks, described in Dizon *et al.* (1992). With the exception of the three stocks of *Stenella attenuata* and the one stock of *Stenella coeruleoalba*, these were the same stocks used in Wade and Gerrodette (1992). The rest of the stocks represent species level estimates, with the exception of two genus level categories. Abundance estimates were made for three additional species of dolphin (i.e. members of the subfamily Delphininae or Steninae), one genus and four species in the subfamily Globicephalinae, two species in the superfamily Physeteroidea, one species and one genus in the family Ziphiidae, and two species in the family Balaenoptera.

*Subfamily* **Delphininae**

*Stenella attenuata*

Abundance estimates were made for three spotted dolphin stocks: the coastal spotted stock (subspecies *S. attenuata grafmani*); and two offshore stocks, the northeastern spotted and western/southern spotted, using the stock boundaries of Dizon *et al.* (1992) shown in Fig. 2.* This was a substantial revision of the offshore stock boundaries described in Perrin *et al.* (1985), based on a re-examination of cranial morphology (Perrin *et al.*, 1991). The northeastern spotted dolphin (378 sightings) has a stock area that corresponds to the inshore and middle strata, with the exception that the southern boundary is at 5°N, rather than at 1°S (Fig. 2; dashed line is dividing line between the two stocks). The western/southern spotted dolphin (210 sightings) has a stock area that is both to the south and the west of the northeastern stock area, and corresponds to the south stratum (previously the southern spotted stock area) combined with the west stratum and the portions of the inshore and middle strata south of 5°N. The coastal spotted dolphin (16 sightings) has a stock area which is a narrow band 185km (100 n.miles) offshore along the Central American and Mexican coast (Fig. 2; solid line), and is entirely contained within the offshore stock areas.

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* Figures 2 to 19 are at the end of the paper.

*Stenella longirostris*
Abundance estimates were made for two stocks of spinner dolphin: eastern spinner and whitebelly spinner (Dizon *et al.*, 1992; Fig. 3). The eastern stock of spinner dolphin (236 sightings) is considered a subspecies, *S. longirostris orientalis,* endemic to the ETP, while the whitebelly stock of spinner dolphin (154 sightings) is considered a hybrid between the eastern spinner and the pantropical spinner dolphin, *S. longirostris longirostris* (Perrin, 1990). The eastern and whitebelly stocks have a considerable region of overlap in their stock areas (Fig. 3; eastern stock, dotted line; whitebelly stock, dashed line). There were no sightings during the surveys of the Central American spinner dolphin, *S. longirostris centroamericanus,* as very little survey effort was spent in its distribution area, which is within 80km of the Central American coast (Fig. 3; solid line).

*Stenella coeruleoalba*
Abundance estimates were made for one stock of striped dolphin, from a total of 799 sightings (Fig. 4). Earlier work suggested that there were geographical stocks of striped dolphin in the eastern tropical Pacific (Perrin *et al.*, 1985). However, recent investigations indicate they should be considered as one stock (Dizon *et al.*, 1992).

*Delphinus delphis*
Abundance estimates were made for three stocks of common dolphin: northern common; central common; and southern common (Dizon *et al.*, 1992). These also correspond to the recommended management units of Perrin *et al.* (1985). The dividing lines relative to the study area between the northern (47 sightings) and central (70 sightings) stocks, and between the central and southern (92 sightings) stocks, are shown in Fig. 5 (dashed lines).

A fourth stock, the Baja neritic common dolphin (Perrin *et al.*, 1985), occurs within the northern stock area within 100 n.miles of the coast of Baja California, Mexico. Recent morphological and genetic evidence suggests that the two sympatric forms, referred to as the shortbeak (or offshore) form and the longbeak (or Baja neritic) form, are sufficiently different to deserve separate species status (Heyning and Perrin, 1991; Dizon *et al.*, 1992; Rosel *et al.*, In press). The shortbeak appears synonymous with *Delphinus delphis* while the longbeak form appears to be equivalent to the nominal species *Delphinus bairdii*. Criteria sufficient to distinguish the two forms in the field were not established until the last year of the surveys; consequently, only one identified sighting of the longbeak form was made in the study area (Fig. 5). Since insufficient information existed to distinguish sightings of the two forms for most of the surveys, all sightings within the northern stock area were pooled.

*Lagenodelphis hosei*
An abundance estimate was made for one stock of the Fraser's dolphin, from a total of 25 sightings (Fig. 6).

*Tursiops truncatus*
An abundance estimate was made for one stock of the bottlenose dolphin, from a total of 298 sightings (Fig. 7). Although it has been suggested that there are coastal and offshore forms of *Tursiops* in the eastern Pacific (Walker, 1981), there has been no conclusive study to establish stock areas or criteria for identifying the stocks in the field.

*Grampus griseus*
An abundance estimate was made for one stock of the Risso's dolphin, from a total of 194 sightings (Fig. 8).

*Other delphinids*
Due to the small number of sightings and the fact that most of its range was to the north of the study area, no abundance estimate was made for the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, for which there were 13 sightings at the northern extreme and north of the study area (Fig. 6). Similarly, no abundance estimate was made for the dusky dolphin, *Lagenorhynchus obscurus*, for which there was one sighting just south of the southern extreme of the study area (Fig. 6).

*Subfamily* **Steninae**
*Steno bredanensis*
An abundance estimate was made for one stock of the rough-toothed dolphin, from a total of 135 sightings (Fig. 9).

*Subfamily* **Globicephalinae**
*Globicephala sp.*
An abundance estimate was made for one stock of the pilot whales, from a total of 222 sightings (Fig. 10). This stock was referred to as *Globicephala* sp., although the majority of the sightings were probably *G. macrorhynchus*. An unknown quantity of sightings of *G. melas* were probably encountered at the southern extreme of the study area in the Peru current, but identification in the field is not possible, hence the designation of *Globicephala* sp.

*Peponocephala electra*
An abundance estimate was made for one stock of the melon-headed whale, from a total of 14 sightings (Fig. 6).

*Pseudorca crassidens*
An abundance estimate was made for one stock of the false killer whale, from a total of 34 sightings (Fig. 11).

*Feresa attenuata*
An abundance estimate was made for one stock of the pygmy killer whale, from a total of 29 sightings (Fig. 11).

*Orcinus orca*
An abundance estimate was made for one stock of the killer whale, from a total of 57 sightings (Fig. 11).

*Family* **Ziphiidae**
*Ziphius cavirostris*
An abundance estimate was made for one stock of Cuvier's beaked whale, from a total of 91 sightings (Fig. 12).

*Mesoplodon* sp.
An abundance estimate was made for one stock of *Mesoplodon* sp. There were 125 total *Mesoplodon* sightings including 88 sightings unidentified to species (Fig. 13). The remaining 37 sightings were distributed among three species: 19 sightings of a possibly un-named *Mesoplodon* sp. (Pitman *et al.*, 1987; sp. 'A' in Fig. 13); 12 sightings of Blainville's beaked whale, *Mesoplodon densirostris*; and three sightings of the recently named pygmy beaked whale, *Mesoplodon peruvianus* (Reyes *et al.*, 1991). It is not clear whether the relative abundance of species of *Mesoplodon* was reflected in the frequency of species identification. *Mesoplodon* sp. 'A' was possibly identified the highest percentage of the time, as the

substantial white chevron that is seen on larger animals is visible at a great distance (Pitman *et al.*, 1987). Information on how to identify the new species *M. peruvianus* was not available to the observers until during the 1988 survey, so it is likely that several sightings of this species were called unidentified *Mesoplodon* prior to that time. Its small size and short beak (Reyes *et al.*, 1991) may have made it relatively easy to identify since then. *M. densirostris* was only definitively identified when an excellent view of the head was obtained, allowing a view of the teeth or the high arching mouth-line. It is likely that it was identified the lowest percentage of the time, and the majority of unidentified *Mesoplodon* may therefore have been *M. densirostris*. Since the different species are likely to have had different probabilities of being identified, only a pooled abundance estimate for *Mesoplodon* sp. was made.

### *Other ziphiids*

Due to the small number of sightings, no abundance estimates were made for the Southern bottlenose whale, *Hyperoodon* sp. cf *H. planifrons*, for which there were four sightings, or for Baird's beaked whale, *Berardius bairdii*, for which there were two sightings (Fig. 14).

### *Superfamily* **Physeteroidea**

### *Physeter macrocephalus*

An abundance estimate was made for one stock of the sperm whale, from a total of 148 sightings (Fig. 15).

### *Kogia simus*

An abundance estimate was made for one stock of the dwarf sperm whale, of which there were 84 sightings (Fig. 16). There were an additional 11 sightings which were identified as being either *K. breviceps* (pygmy sperm whale) or *K. simus*. *K. breviceps* is thought to have a more northerly distribution than *K. simus* (Leatherwood *et al.*, 1988), and during the survey, *K. breviceps* was only sighted four times in the study area. These four sightings were all north of 24°N, close to the boundary of the study area, while all *K. simus* sightings were south of 24°N, indicating agreement with the suggested distribution (Fig. 16). All unidentified *Kogia* sightings south of 24°N (a total of 10) were therefore considered *Kogia simus* for the abundance estimate, for a total of 95 sightings. There was one unidentified *Kogia* sighting north of 24°N that was not used in the abundance estimate. No abundance estimate was made for *Kogia breviceps*.

### *Family* **Balaenopteridae**

### *Balaenoptera musculus*

An abundance estimate was made for one stock of the blue whale, from a total of 31 sightings (Fig. 17).

### *Balaenoptera edeni*

An abundance estimate was made for one stock of the Bryde's whale. There were 42 confirmed sightings of *B. edeni* where the auxiliary ridges on the head were seen, a character which distinguishes this species from *B. borealis*, the sei whale (Leatherwood *et al.*, 1988) (Fig. 18). There were also 67 sightings identified as being either *B. edeni* or *B. borealis*, where the head was not seen well enough to determine if the auxiliary ridges were present or not. B. borealis is known to have a more northerly, temperate distribution in the eastern Pacific (Leatherwood *et al.*, 1988). Therefore, the 67 *B. edeni*/*B.* borealis sightings were considered *B. edeni* for this abundance estimate, for a total of 109 sightings.

### *Other rorquals*

Due to the small number of sightings, no abundance estimates were made for the three other species of rorqual seen during the surveys. There were 14 sightings of the humpback whale, *Megaptera novaeangliae*, six sightings of the minke whale, *B. acutorostrata* and one sighting outside of the study area of the fin whale, *B. physalus* (Fig. 17).

### **Abundance estimation**

The same methodology as in Wade and Gerrodette (1992) was used, with minor exceptions, but was applied to the pooled data set of all five years, rather than to each year separately. Estimates of population abundance ($N_j$) of stock *j* were computed by line-transect methods (Burnham *et al.*, 1980; Hiby and Hammond, 1989) as:

$$N_j = \sum_{k=1}^{4} N_{jk} \tag{1}$$

where

$$N_{jk} = \frac{n_{jk} f_j(0)}{2L_k} \tag{2}$$

and

$N_{jk}$ = abundance estimate of stock *j* in stratum *k*,
$n_{jk}$ = number of schools of stock *j* in stratum *k*,
$f_{jk}(0)$ = detection function of stock *j* in stratum *k*, evaluated at zero distance,
$S_{jk}$ = mean school size of stock j in stratum *k*,
$L_k$ = total effort in stratum *k* in kilometers,
$A_k$ = total area in stratum k in square kilometers.

This represents a stratified analysis, where only cetacean sightings from stock *j* were used to calculate the density and therefore abundance of stock *j* within stratum *k*, with the abundance summed across the four strata for a total estimate for the stock.

In Wade and Gerrodette (1992), data were pooled across strata for the estimation of *f*(0). The increased quantity of data obtained by pooling across years allowed, in some cases, a fully stratified analysis, where *f*(0) was calculated separately for each stratum. However, not all stocks had enough sightings in every stratum. Therefore, where less than 50 sightings existed in a stratum, data were pooled across strata for the calculation of *f*(0) until more than 50 sightings were available. The inshore and middle strata had similar levels of effort per unit area (9.3 and 10.1km/1000km$^2$, respectively), as did the west and south strata (3.7 and 5.6km/1000km$^2$, respectively). Therefore, where possible, these strata were pooled first. Details for each stock are explained below. A hazard rate model (Hayes and Buckland, 1983; Buckland, 1985) was fitted to the data to estimate $f_{jk}(0)$.

The standard error of $N_j$ was estimated using bootstrap methods (Efron, 1982). Within each stratum and year, the total distance of searching effort was tabulated, and then legs of effort were randomly selected with replacement until that amount of effort was equaled. This effort and the associated sightings were then pooled across years and used to calculate $f_{jk}(0)$, $S_{jk}$, $n_{jk}$ and finally $N_j$. This process was repeated 1,000 times. The standard error and coefficient of variation of $N_j$ were calculated using these 1,000 estimates. A 95% confidence interval on $N_j$ was estimated by the central 95% of the bootstrap estimates.

### **Proration of unidentified sightings**

There were a number of sightings that were not identified to a stock but were identified to a broader category. Abundance estimates for these unidentified categories were prorated to every stock that was included in the broader category. A full description of the stocks in each category will follow. The general method used to calculate a revised abundance estimate $N_j^*$ for stock $j$ by prorating the sighting from these unidentified categories was:

$$N_j^* = \sum_{k=1}^{4} N_{jk}^* \qquad (3)$$

where

$$N_{jk}^* = N_{jk} + N_{uk}\left(\frac{N_{jk}}{N_{jk} + \sum_{i=1}^{m} N_{ik}}\right) \qquad (4)$$

and

$N_{jk}^*$ = revised abundance estimate for stock $j$ in stratum $k$,
$N_{jk}$ = abundance estimate for stock $j$ in stratum $k$ using only identified sightings of stock $j$ (from Eq. 1),
$N_{uk}$ = abundance estimate for the unidentified category containing stock $j$ in stratum $k$,
$N_{ik}$ = abundance estimate(s) for other stock(s) also contained in the unidentified category in stratum $k$,
$m$ = number of additional stocks also contained in the unidentified category.

Within each stratum, this represents a proration of the unidentified abundance estimate to each stock based on the ratio of the abundance estimate of that stock divided by the sum of the abundance estimates of all the stocks in that unidentified category. This proration method assumes that all stocks within a category had an equal probability of being unidentified when seen. There were six different unidentified categories, described below.

*(1) Unidentified spotted dolphins*

The northeastern stock of offshore spotted dolphin partially overlaps the range of coastal spotted dolphins, which extends out 185km (100 n.miles) from the west coast of Central America (Fig. 2; Perrin *et al.*, 1985). There were seven unidentified spotted dolphin sightings that occurred within the overlap region. An abundance estimate based on those seven sightings was prorated between these two stocks, using an $f(0)$ calculated from all spotted dolphin sightings within this overlap region. Eq. 4 was modified slightly to use an abundance estimate for northeastern spotted dolphins just within the overlap region with the coastal stock area. The range of the coastal spotted dolphin also partially overlaps the range of the western/southern stock of offshore spotted dolphin. No coastal spotted dolphins were seen in this overlap region during the surveys; therefore the one unidentified spotted sighting within this region was allocated to the western/southern stock of offshore spotted dolphin.

*(2) Unidentified spinner dolphins*

There were 16 unidentified spinner dolphin sightings within the region of overlap between the eastern and whitebelly stock areas (Fig. 3). An abundance estimate based on these 16 sightings was prorated between the two stocks, using an $f(0)$ calculated from all spinner dolphin sightings with the region of overlap. As in the case for unidentified spotted dolphins, Eq. 4 was modified slightly by using abundance estimates for the eastern and whitebelly stocks calculated just within the area of overlap, rather than abundance estimates from the entire stratum.

*(3) Unidentified dolphin sightings*

Sightings not identified to species or stock but known to be a dolphin due to body size or the presence of a distinct beak were categorized as unidentified dolphins. These were sightings that were lost before an adequate identification was made. Generally these represented sightings that were small in school size or were sighted at a large distance from the ship, or both. There were 701 of these sightings, from which an unidentified dolphin abundance estimate was made. This abundance estimate was prorated among the fourteen stocks in the Delphininae and Steninae: *Stenella* sp. (six stocks); *Delphinus delphis* (three stocks); *Lagenodelphis hosei*, *Tursiops truncatus; Steno bredanensis;* and *Grampus griseus*. The only other dolphin seen in the study area was the Pacific white-sided dolphin, *Lagenorynchus obliquidens*, of which there were only three sightings available for an abundance estimate, all at the northern extreme of the study area close to the coast of Baja, Mexico (Fig. 6). These sightings were ignored for this proration of unidentified dolphin sightings.

*(4) Unidentified Ziphiids (beaked whales)*

Over 97% of the 225 beaked whale sightings identified to genus or species were *Mesoplodon* (128) or *Ziphius cavirostris* (91) sightings. The other species identified were a bottlenose whale, *Hyperoodon* sp. cf H. *planifrons* (4) and Baird's beaked whale, *Berardius bairdii* (2). There were a total of 104 unidentified Ziphiid sightings, which could be prorated among all four stocks. However, the six sightings of *Hyperoodon* sp. and *Berardius bairdii* represent less than 3% of the total number of beaked whales identified to genus, and were ignored for this calculation. The abundance estimate for unidentified Ziphiids was therefore prorated between the two stocks of *Ziphius cavirostris* and *Mesoplodon* sp.

*(5) Unidentified Balaenopteridae (rorquals)*

Some whale sightings could be identified as rorquals, but were not identified to species. There were 97 of these sightings, categorized as unidentified Balaenopteridae (Fig. 19). Although all six rorqual species were seen during the surveys, only two, *B. edeni* (109 sightings) and *B. musculus* (31 sightings), were seen with enough frequency to estimate their abundance. The numbers of sightings of other rorquals were six humpback whales, *Megaptera novaeangliae*, six minke whales, *B. acutorostrata*, and one sighting of the fin whale, *B. physalus* north of the study area, which were insufficient numbers from which to estimate abundance, as required in Eq. 4. Therefore, Eq. 4 was modified slightly to prorate unidentified Balaenopteridae to *B. edeni* and *B. musculus*. The summation in the denominator on the right side of Eq. 4 was replaced by a pooled abundance estimate based on all rorqual sightings identified to species, excluding sightings of stock $j$. For example, for *B. edeni*, the summation was replaced by a pooled estimate from the sightings of *B. musculus*, *B. acutorostrata*, and *M. novaeangliae*, for a total of 44 sightings. Similarly, for *B. musculus*, the summation was replaced by a pooled estimate from the sightings of *B. edeni*, *B. acutorostrata*, and *M. novaeangliae*, for a total of 121 sightings.

*(6) Unidentified large whales*

There were also 82 whale sightings which were determined to be either sperm whales or rorquals but were not identified to species. These were termed unidentified large whales, and an abundance estimate from these sightings was prorated between sperm whales and rorquals. Again, abundance estimates were not available for the infrequently seen rorqual species, so a pooled estimate for all rorqual sightings was used to prorate this abundance estimate between *P. macrocephalus* and all rorquals, using Eq. 4. The amount prorated to all rorquals was further prorated to *B. edeni* and *B. musculus*, using the same term in parentheses on the right hand side of Eq. 4 as was used in prorating the unidentified Balaenopteridae sightings described in the previous section.

## RESULTS AND DISCUSSION

A total of 135,324km of on-effort trackline was surveyed during the five years (Table 1) and approximately 4,600 cetacean sightings contributed to the abundance estimates. This resulted in an encounter rate of 32.2 cetacean schools per 1,000km. Total density of cetaceans in the ETP was estimated as 0.52 animal per km$^2$.

Table 1

Eastern tropical Pacific study area and survey effort. Area $A_k$ (in thousands of square kilometers, from Holt and Sexton 1990a), % of total study area, achieved survey effort $L_k$ (in thousands of kilometers) in each stratum, summed over the 5 surveys from 1986-90, % effort achieved in each stratum, and the target % effort as calculated in Holt *et al.* 1987.

| | Inshore | Middle | West | South | Total |
|---|---|---|---|---|---|
| Area (1000km$^2$) | 5693.0 | 3798.0 | 5298.0 | 4359.0 | 19148.0 |
| Percent of Total | 29.7 | 19.8 | 27.7 | 22.8 | 100.0 |
| Effort (1000km) | 52.8 | 38.0 | 19.8 | 24.4 | 135.3 |
| Percent | 39.0 | 28.3 | 14.6 | 18.0 | 100.0 |
| Target percent | 35.8 | 28.7 | 14.0 | 21.5 | 100.0 |

Abundance estimates for all 24 stocks, both before and after proration, are summarized in Table 2. Abundance estimates totaled 9.6 million animals for all species in the subfamilies Delphininae and Steninae (dolphins), 292,800 for all species in the subfamily Globicephalinae, 45,300 for all species in the family Ziphiidae (beaked whales), 33,881 for all species in the superfamily Physeteroidea (sperm and pygmy sperm whales) and 14,431 for both species in the family Balaenopteridae (rorquals).

The most numerous species was estimated to be *Delphinus delphis*, as the three stocks summed to 3,100,000, with the majority in the southern stock. When the three *Stenella* species were summed across stocks, each was estimated at 1,600,000–2,100,000 animals. In total, these four species were estimated to number 8,700,000. Estimated dolphin density (in animals per km$^2$) was 0.50 for the entire study area, and was highest in the south stratum (0.70), followed by the inshore (0.55), the west (0.38) and finally the middle stratum (0.35). The total estimated number of dolphin schools in the study area was 103,828, which represents a school density of 0.0054/km$^2$, or one school/185km$^2$.

The highest estimate for an individual stock was for the southern common dolphin, estimated at 2,100,000 with relatively large confidence limits. The second highest estimate was for the striped dolphin at 1,900,000, followed by the western/southern offshore spotted dolphin (1,300,000) and the whitebelly spinner dolphin (1,000,000).

Excluding the four most abundant species, the next highest dolphin estimates were for *Lagenodelphis hosei* (281,000) and *Tursiops truncatus* (226,200). The highest estimate for a small whale was for the pilot whale, *Globicephala* sp. (160,200); only 8,500 killer whales, Orcinus orca, were estimated to be in the ETP. Coefficients of variation (CV) ranged from 0.112 (*Stenella coeruleoalba*) to 0.636 (*Pseudorca crassidens*), with most being less than 0.40.

The most frequently encountered cetacean species was *Stenella coeruleoalba*, which was seen at the rate of 5.4 schools per 1,000km, followed by *S.attenuata* (4.1/1,000km) and *S.longirostris* (2.8/1,000km). The most frequently encountered small whale was *Globicephala* sp. (1.7/1,000km), while the most frequently encountered large whale was *Physeter macrocephalus* (1.0/1,000km).

### Comparisons with previous estimates

The eastern tropical Pacific Ocean is a distinct oceanographic region characterized by a shallow thermocline and relatively high production (Fiedler *et al.*, 1991). The extensive line-transect efforts summarized here have produced the most comprehensive mammal and bird surveys ever undertaken in this part of the ocean. The estimates combine sightings between 1986 and 1990, and thus represent cetacean abundance averaged over five years. Annual estimates of dolphin abundance vary considerably from year to year (Buckland *et al.*, 1992; Wade and Gerrodette, 1992). Such interannual variability in the estimates is due to both sampling variability and to oceanographic variability associated with the El Niño-Southern Oscillation (Fiedler *et al.*, 1992).

For most of the species in this report (with the exception of the dolphins caught in the tuna fishery), previous estimates of abundance in tropical waters have been crude, or not possible at all from occasional sightings. The estimates of abundance in Table 2 are based on surveys specifically designed for marine mammals. Because the estimates are based on a statistical model, a coefficient of variation (CV; the ratio of the standard error to the point estimate ) and a confidence interval are calculated for each estimate. The precision of the estimates of abundance varies considerably, with CVs ranging from 0.112 to 0.636. Estimates for the more frequently seen species tend to have lower CVs and shorter confidence intervals.

The most common cetaceans on these surveys were the spotted, spinner, common and striped dolphins. The large number of sightings made it possible to estimate population sizes separately for several stocks of these species. No estimate of the Central American subspecies of spinner dolphins (Perrin, 1990) was possible because our surveys had little effort in the limited area where that subspecies occurs (Fig. 3). We do compute an estimate for another geographically restricted subspecies, the coastal spotted dolphin, but we consider this estimate somewhat questionable because the distribution of search effort in its range near the coastline (Fig. 2) was not completely random, but tended to be concentrated near ports.

Total dolphin density was highest in the south stratum during these surveys. Previous estimates of abundance have generally shown highest dolphin school density near the Mexican and Central American coastline (Holt *et al.*, 1987; Polacheck, 1987), the inshore stratum in these surveys. Purse-seining has operated most intensively in this area, and historically the highest dolphin kills have been on the stocks that occur here, the northeastern spotted and eastern spinner dolphins (Smith, 1983). However, whether

Table 2

Abundance estimates for eastern tropical Pacific cetaceans in thousands of animals. $N_j$ is the estimate based only on identified sightings of the stock. $N_j$*(int) represents intermediate pro-rated abundance estimates from three unidentified categories involving 6 stocks. $N_j$* represents final abundance estimates, some of which were pro-rated from three unidentified categories. Note that the abundance estimates for species in the *Globicephalinae* and *Kogia simus* did not involve any pro-rating. CV represents the coefficient of variation for $N_j$*. $N_j$*U and $N_j$*L represent, respectively, the upper and lower 95% bootstrap confidence limits, calculated using the percentile method (Efron 1982).

| | $N_j$ | $N_j$*(int) | $N_j$* | CV | $N_j$*$_L$ | $N_j$*$_U$ |
|---|---|---|---|---|---|---|
| Delphininae | | | | | | |
| *Stenella attenuata* | | | | | | |
| Northeastern spotted | 663.3 | 668.8 | 730.9 | 0.142 | 588.7 | 970.4 |
| Western/southern spotted | 1258.9 | | 1298.4 | 0.150 | 918.7 | 1654.1 |
| Coastal spotted | 25.6 | 27.2 | 29.8 | 0.346 | 15.1 | 50.8 |
| *Stenella longirostris* | | | | | | |
| Eastern spinner | 568.1 | 583.5 | 631.8 | 0.238 | 389.5 | 938.3 |
| Whitebelly spinner | 988.6 | 992.2 | 1019.3 | 0.187 | 694.4 | 1456.2 |
| *Stenella coeruleoalba* | 1824.5 | | 1918.0 | 0.112 | 1531.8 | 2249.3 |
| *Delphinus delphis* | | | | | | |
| Northern common | 433.7 | | 476.3 | 0.367 | 200.6 | 807.3 |
| Central common | 371.2 | | 406.1 | 0.383 | 200.3 | 766.0 |
| Southern common | 2127.7 | | 2210.9 | 0.217 | 1536.6 | 3488.2 |
| *Lagenodelphis hosei* | 281.5 | | 289.3 | 0.335 | 138.0 | 508.1 |
| *Tursiops truncatus* | 226.2 | | 243.5 | 0.286 | 190.9 | 409.9 |
| *Grampus griseus* | 164.1 | | 175.8 | 0.381 | 90.0 | 375.4 |
| Steninae | | | | | | |
| *Steno bredanensis* | 136.7 | | 145.9 | 0.320 | 89.4 | 256.8 |
| Globicephalinae | | | | | | |
| *Globicephala* sp. | | | 160.2 | 0.138 | 112.3 | 198.4 |
| *Peponocephala electra* | | | 45.4 | 0.467 | 34.2 | 110.3 |
| *Feresa attenuata* | | | 38.9 | 0.305 | 18.5 | 63.1 |
| *Pseudorca crassidens* | | | 39.8 | 0.636 | 11.5 | 109.5 |
| *Orcinus orca* | | | 8.5 | 0.368 | 4.7 | 15.9 |
| Ziphiidae | | | | | | |
| *Ziphius cavirostris* | 16.1 | | 20.0 | 0.265 | 13.8 | 34.5 |
| *Mesoplodon* sp. | 20.2 | | 25.3 | 0.195 | 17.4 | 34.4 |
| Physeteroidea | | | | | | |
| *Physeter macrocephalus* | 21.2 | | 22.7 | 0.224 | 14.8 | 34.6 |
| *Kogia simus* | | | 11.2 | 0.294 | 7.7 | 16.2 |
| Balaenopteridae | | | | | | |
| *Balaenoptera musculus* | 1.1 | 1.3 | 1.4 | 0.243 | 1.1 | 2.5 |
| *Baleanoptera edeni* | 9.9 | 12.0 | 13.0 | 0.202 | 8.9 | 19.9 |

there have been shifts in dolphin species composition and abundance and, if so, whether such changes are due to the incidental kill in the tuna fishery is uncertain.

The five-year combined estimates for spotted, spinner, striped, and common dolphins are close to, but not the same as, the average of the annual estimates of abundance for these species based on the same surveys (Wade and Gerrodette, 1992). The differences are due to (a) pooling data over all five years, (b) including unidentified sightings by proration, (c) changing stock definitions for the spotted and striped dolphins, and (d) slight changes in the data selection criteria. Populations of several stocks, notably the northeastern spotted and eastern spinner dolphins, have been considerably reduced as a result of mortality in tuna purse-seine nets (Smith, 1983; Wade, 1993), but indications are that populations have not, in general, been decreasing over the last ten years (Buckland *et al.*, 1992; Wade and Gerrodette, 1992).

Omura and Ohsumi (1974) estimated 1,340 blue whales in the North Pacific in 1970, and Wada (1975) estimated 1,600 whales for the 1973 season. These numbers were subsequently summarized by Gambell (1976) and most recently by Braham (1991). We estimate 1,415 blue whales in the eastern tropical Pacific area, with a 95% confidence interval from 1,078 to 2,501. The non-overlap in study area makes comparison with previous estimates difficult. The tropical blue whales may represent a second population center in the north Pacific Ocean, or they may be the same whales migrating seasonally between high and low latitudes. Because the surveys reported here took place from late July to November, one might expect that Northern Hemisphere blue whales would be at their high latitude feeding grounds during our surveys. The blue whales seen in our study area might thus represent a year-round population in high productivity areas (Reilly and Thayer, 1990) or, possibly, migrants from the Southern Hemisphere winter.

A ship survey in 1991 off the coast of California using the same procedures as described here has produced an estimate of 2,332 blue whales (J. Barlow, pers. comm., Southwest Fisheries Science Center, National Marine Fisheries Service, La Jolla, CA, 92308, USA). Because this survey took place at the same time of year as the ETP surveys, a minimum estimate of blue whale abundance in the eastern Pacific is the sum of these two point estimates, or 3,779 blue whales. An August ship survey and aerial surveys throughout the year did not find any blue whales off the coast of Oregon and Washington (Green *et al.*, 1992).

Many of the same comments apply when trying to interpret our estimate of sperm whale abundance. Recent estimates of the number of mature sperm whales in the eastern North Pacific are about 275,000 (Gosho *et al.*, 1984). Our total population estimate of approximately

23,000 with a 95% confidence interval of 14,791 to 34,639 is an order of magnitude lower, but applies to a different area. Sperm whales also undergo seasonal migrations, so the presence of these sperm whales in tropical water from August to November may, as with blue whales, either indicate a small resident tropical population or migrants from the Southern Hemisphere.

Based on sightings from commercial tuna vessels, Polacheck (1987) computed cetacean school encounter rates (schools encountered per 1,000 n.miles searched) in the eastern tropical Pacific. To produce an estimate of abundance from a school encounter rate one must also have estimates of school size and effective strip width (Eq. 1). Because both school size and effective strip width may differ by species, time and area, using school encounter rate as an index of relative abundance can be misleading. In Table 3 we have computed weighted mean school size, effective strip width (related to the ease of sighting each species) and the school encounter rate.

Although Polacheck's (1987) data were collected 10 years earlier, some comparisons of school encounter rates are interesting. For comparative purposes, we averaged the encounter rates over the four years of Polacheck's table 2 and converted from nautical miles to kilometers. For the three main dolphin species that associate with tuna and are therefore of primary interest to the tuna fishermen (spotted, spinner, and common dolphins), school encounter rates given by Polacheck are higher than our rates. For other cetacean species not used by the fishery, encounter rates given by Polacheck are all lower than our rates. These differences are probably related to the efficiency with which fishermen can find and report cetaceans of interest to them.

### School sizes and effective strip widths

Although the stratified Equation 1 was used to calculate these abundance estimates, for ease of inspection and comparison between stocks, summary estimates of the parameters of Equation 1 are presented in Table 3. School size, f(0), and encounter rate are presented as mean values for the entire study area, calculated as appropriate weighted means of the four stratum values. Note that the parameter $f(0)$ is expressed as the 'effective strip width' (ESW) in km, which is equal to twice the inverse of $f(0)$. The hazard rate model provided an adequate fit to the data for estimating $f(0)$ in all cases except two: for *Pseudorca crassidens* (pooled estimate across all strata using 34 sightings, $p<0.05$, 1-tailed test, chi$^2$ = 15.91, df=8) and for one of two estimates of $f(0)$ for *Tursiops truncatus* (pooled estimate for the inshore and middle strata using 227 sightings, $p<0.01$, 1-tailed test, chi$^2$ = 20.88, df = 8).

The range in mean school sizes observed during these surveys is striking, ranging from just over two for *Ziphius cavirostris*, to nearly 500 for the southern stock of common dolphins (Table 3). The mean school size estimates may be positively biased because small schools are more likely to be missed than large ones. At least for the schooling dolphins, school size is a dynamic feature of behavior, changing with time of day (Scott and Cattanach,

Table 3

Mean school size, effective strip width in km (ESW, equal to 1/f(0) times 2), number of sightings going into the estimate of school density (n), and the school encounter rate per 1000km (ER). School size, effective strip width, and encounter rate are weighted mean values for the entire study area. Coefficients of variation for the estimates of school size and effective strip width are in parentheses.

| | School size | ESW | n | ER |
|---|---|---|---|---|
| Delphininae | | | | |
| *Stenella attenuata* | | | | |
| Northeastern spotted | 115.9 (0.09) | 6.97 (0.11) | 378 | 2.09 |
| Western/southern spotted | 149.4 (0.08) | 4.27 (0.13) | 210 | 1.88 |
| Coastal spotted | 75.0 (0.15) | 5.04 (0.24) | 16 | 0.09 |
| *Stenella longirostris* | | | | |
| Eastern spinner | 111.7 (0.09) | 5.17 (0.17) | 236 | 1.34 |
| Whitebelly spinner | 134.1 (0.16) | 3.70 (0.13) | 154 | 1.47 |
| *Stenella coeruleoalba* | 60.9 (0.05) | 3.40 (0.09) | 799 | 5.39 |
| *Delphinus delphis* | | | | |
| Northern common | 385.9 (0.23) | 4.47 (0.37) | 47 | 0.26 |
| Central common | 254.4 (0.13) | 5.70 (0.36) | 70 | 0.43 |
| Southern common | 472.8 (0.11) | 2.99 (0.21) | 92 | 0.70 |
| *Lagenodelphis hosei* | 394.9 (0.20) | 6.06 (0.32) | 25 | 0.23 |
| *Tursiops truncatus* | 22.7 (0.22) | 3.85 (0.22) | 298 | 1.98 |
| *Grampus griseus* | 11.8 (0.08) | 1.89 (0.38) | 194 | 1.45 |
| Steninae | | | | |
| *Steno bredanensis* | 14.7 (0.18) | 1.78 (0.19) | 135 | 0.86 |
| Globicephalinae | | | | |
| *Globicephala* sp. | 18.3 (0.08) | 3.70 (0.13) | 222 | 1.70 |
| *Peponocephala electra* | 199.1 (0.20) | 8.26 (0.36) | 14 | 0.10 |
| *Feresa attenuata* | 27.9 (0.12) | 2.83 (0.20) | 29 | 0.21 |
| *Pseudorca crassidens* | 11.4 (0.12) | 1.72 (0.75) | 34 | 0.31 |
| *Orcinus orca* | 5.4 (0.09) | 5.28 (0.31) | 57 | 0.43 |
| Ziphiidae | | | | |
| *Ziphius cavirostris* | 2.2 (0.06) | 1.71 (0.27) | 91 | 0.67 |
| *Mesoplodon* sp. | 3.0 (0.11) | 2.52 (0.14) | 128 | 0.88 |
| Physeteroidea | | | | |
| *Physeter macrocephalus* | 7.9 (0.17) | 7.30 (0.16) | 148 | 1.02 |
| *Kogia simus* | 1.7(0.07) | 1.81 (0.15) | 95 | 0.61 |
| Balaenopteridae | | | | |
| *Balaenoptera musculus* | 1.5 (0.13) | 5.19 (0.19) | 31 | 0.20 |
| *Baleanoptera edeni* | 1.7 (0.07) | 2.70 (0.27) | 109 | 0.84 |

Submitted) and sometimes dramatically between years (Wade and Gerrodette, 1992).

The species with the largest average school sizes were *Delphinus delphis* and *Lagenodelphis hosei*, with mean school sizes all above 250 animals, and as high as 473 for the southern stock of *D. delphis*. Both offshore *Stenella attenuata* stocks, as well as both *Stenella longirostris* stocks, had mean school sizes above 110 animals. Since many of the spotted and spinner schools were actually part of the same school (70% of spinner schools were with spotted dolphins, while 50% of offshore spotted schools were with spinner dolphins), many of these schools numbered more than 300 animals. All four of these dolphin species were seen in schools greater than 1,000 animals, with the largest schools seen estimated to be about 4,000 for *D. delphis*, 2,400 for *S. attenuata*, 1,700 for *S. longirostris*, and 1,500 for *L. hosei*. The striped dolphin occurs in much smaller schools than its congeners, but was the most frequently encountered dolphin on our surveys, particularly in the south. The only other species with an average school size of more than 100 was *Peponocephala electra*, with a mean school size of nearly 200. Many of these schools of melon-headed whales were found in association with large schools of *L. hosei*, the Fraser's dolphin, forming some of the largest mixed-species cetacean schools observed during the surveys. For the larger whale species, mean group sizes were much smaller (approximately 8 for *Physeter macrocephalus*, 5 for *Orcinus orca*, 3 for *Mesoplodon* beaked whales, 2 for *Ziphius cavirostris, Balaenoptera edeni* and *Kogia simus,* and 1.5 for *Balaenoptera musculus*).

In line-transect theory, $f(0)$ is the value of the probability-density function evaluated at zero distance from the trackline. Twice the inverse of this number has an intuitive interpretation as the ESW covered along the trackline, and we have computed this width for each stock in Table 3. The width of this effective strip depends on a number of factors, such as sea state and size and behavior of the animals. A larger ESW means, roughly speaking, that the animals are easier to see, other things being equal. Viewed in this way, the ESW values in Table 3 are generally consistent with what we know of the behavior of the different species. Species that occur in large schools tend to have large ESWs – for example, Fraser's dolphins. The widest effective strip widths, all at more than 6km, were for *Stenella attenuata* (northeastern stock), *Lagenodelphis hosei, Peponocephala electra* and *Physeter macrocephalus. Delphinus delphis* stocks had relatively narrow ESWs considering the large schools in which they usually occur; this may be because common dolphins are not found in association with seabird flocks as often as spotted and spinner dolphins (seabird flocks act as a cue and make the school more likely to be seen).

Not surprisingly, the smallest ESWs in Table 3 belong to the beaked whales and the cryptic *Kogia simus*. Among the delphinids, *Steno bredanensis* and *Grampus griseus* have the narrowest strip widths; these species occur in small schools and are the least 'showy' of the delphinids in their behavior. The small whales are intermediate between these, with ESWs ranging from 1.4 to 3.3km. *Peponocephala electra* has the largest ESW among the small whales, probably due to the large schools in which it is found. *Orcinus orca* occur in small schools, but have prominent dorsal fins and behavior. *Globicephala* sp. also have relatively prominent dorsal fins. The narrowest ESWs among the small whales belong to *Pseudorca crassidens* and *Feresa attenuata*, which have neither prominent fins nor behavior.

The wide ESW for *Physeter macrocephalus* is probably due to its prominent and distinctive blow, and to the fact that it tends to occur in larger groups than the two rorquals. The difference in ESW between *Balaenoptera musculus* and *B. edeni* is probably due to the larger blow of the former.

### Possible bias

Violations of the assumptions of the line-transect model may lead to biases in the estimates of abundance. Of primary concern is the assumption that all animals on the trackline are seen. This is usually expressed in terms of the detection probability $g(x)$ of an animal at distance $x$, with $g(0)=1.0$ meaning that it is certain that an animal on the trackline will be seen (Burnham *et al.*, 1980). If $g(0)$ is less than 1.0, the abundance will be underestimated unless $g(0)$ is explicitly estimated, which was not done here. Our estimates are unadjusted for animals missed on the trackline and are therefore likely to be underestimates of the true population sizes for some species. Although estimates of $g(0)$ are generally species and area specific, estimates for similar species from other studies may give some indication of the magnitude of the potential bias. The assumption that $g(0)=1.0$ is unlikely to be true for sperm and beaked whales because they have long dive times and may not be at the surface during the time the ship passes by. Kasamatsu and Joyce (1991) estimated that $g(0)$ for beaked whales in the Antarctic was 0.25–0.50. Therefore, our estimates of abundance for the beaked whales *Ziphius cavirostris* and *Mesoplodon* sp. and for the sperm whales *Physeter macrocephalus* and *Kogia simus* are likely underestimates, perhaps by as much as one half.

The rorquals (blue and Bryde's whales) may also be missed on the trackline due to submergence when the ship passes close to their position, although their dive times are much less than sperm and beaked whales. An independent-observer experiment estimated $g(0)$ for minke whales off Spitsbergen to be significantly less than 1.0 (Oien, 1990). However, the platform had an obstructed view, which was not the case on our research vessels, so it is uncertain how appropriate these g(0) estimates would be to our abundance estimates for blue and Bryde's whales. Schweder *et al.* (1991) estimated $g(0)$ as 0.43 for northeastern Atlantic minke whales using a parallel ship experiment, and Schweder *et al.* (1992) updated that analysis with additional data to estimate $g$ (0) as 0.506 for the same population. These estimates for minke whales may have some relevance to our estimate of abundance of the slightly larger Bryde's whale. However, the tall visible blow of the blue whale makes it unlikely that they were frequently missed, as they were often seen at a great distance from the ship and probably did not stay submerged the entire time that they were in the field of view of the ship.

None of the other species were likely to stay submerged as a group for significant periods of time. The globicephalids were unlikely to be missed because of their prominent profile at the surface. It is possible that *Steno bredanensis* and *Grampus griseus*, because of their small school size and/or low profile in the water, may be occasionally missed close to the trackline. The smaller delphinids, spotted, spinner, common, striped, Fraser's and bottlenose dolphins, all tend to occur in large schools and have short dive times. It is unlikely that any such schools were missed on the trackline, although it may be possible for some of the smaller schools of striped dolphin. A limited independent-observer experiment during the 1990 cruise indicated that no large schools were missed on the trackline; if small schools are occasionally missed, it will have little effect on the estimates for these species.

For the small delphinids that have a large range in school size, another possible bias arises from the overestimation of mean school size due to the decreased probability of detection of smaller schools at greater perpendicular distance. A preliminary investigation indicated that some of the stocks have a significant relationship between school size and perpendicular distance, while some do not. A linear regression of the logarithm of school size against $g(x)$, the estimated probability of detection (Laake *et al.*, 1993), was performed for one stock from each of the four most abundant dolphin species. The eastern spinner stock did not have a significant regression, and therefore its school size estimate was not apparently biased in this way. However, the other three stocks did have significant regressions, indicating that their school size estimates, and hence abundance estimates, were biased. Estimates of the corrected school sizes were lower by 14% for the northeastern offshore spotted dolphin, 12% for the striped dolphin, and 33% for the central common dolphin. This indicates that there is a small bias for most of the small delphinid stocks, with the possibility of more substantial biases in the estimates of the species that can occur in very large schools, such as the common and the Fraser's dolphin. Future estimates of abundance for these species should fully utilize a school size correction method such as the regression technique used preliminarily here.

The estimate of mean school size may also be biased due to errors by the observers in estimating school size. However, aerial photography during the surveys has shown that, on average, observers estimated school size accurately, although for the largest schools there was a tendency to underestimate school size (Gerrodette and Perrin, 1991). Another source of bias could result from reaction of the dolphins to the ship before detection, leading to a negative bias if they avoided the ship or a positive bias if they were attracted to the ship. To be a significant bias, dolphin schools would have to perceive and react to the ship at a large distance, because the average detection distance from the ship was approximately 5km. Aerial observations on a limited number of ETP dolphin schools have shown that some dolphin schools turn away from the ship at more than this distance, but that most schools are detected by observers before they react to the ship (Au and Perryman, 1982; Hewitt, 1985). Therefore, ship avoidance behavior by the dolphins may result in a small negative bias in the estimates presented here.

In general, the proration of unidentified sightings to the groups in Table 2 had little effect on the estimates. This is because, for most species, unidentified sightings form a small part of the total sightings. The differences between estimates before ($N_j$) and after ($N_j^*$) assignment of the unidentified sightings are most noticeable with the beaked and rorqual whales. The number of unidentified sightings was higher for these species groups because: (1) beaked whales were hard to identify to species in the field, although relatively easy to determine that they belonged to the 'beaked whale' group; and (2) rorquals could be identified as such at a great distance, but the ship did not always 'close' on these sightings. The proration of unidentified rorquals to blue whales, which added about 200 to the abundance estimate (Table 2), may be an overestimate, because the observers were more likely to investigate and identify rorqual sightings with the potential to be a blue whale, such as those exhibiting a large blow.

The surveys were designed to estimate the abundance of pelagic dolphin populations. Consequently, the coast and continental shelf were not systematically surveyed, and may have been proportionally under-represented (Fig. 1). As previously mentioned, the study did not reliably survey the areas inhabited by the coastal spotted and the Central American spinner dolphins. This may also have lead to an underestimate of abundance of the bottlenose dolphin, as it was encountered more frequently very close to shore (Fig. 7). Also affected were probably the sighting rates of some of the rorqual species other than the pelagically distributed Bryde's whale. For example, many of the few humpback whale sightings were very close to the coast (Fig. 17), and humpbacks are known to winter and breed in Mexican waters (Urban and Aguayo-L, 1987) and off Costa Rica (Steiger *et al.*, 1991). Therefore, the distribution maps may not fully describe the occurrence of coastal species throughout the study area, as many coastal areas were not surveyed.

### Distribution

The distributions of the three *Stenella* sp. and *Delphinus delphis* are well known from previous analyses, with *S. attenuata* (Fig. 2) and *S. longirostris* (Fig. 3) most abundant in warm, tropical waters, *D. delphis* (Fig. 5) most abundant in cold, upwelling-modified waters and *S. coeruleoalba* (Fig. 4) most abundant where the other three species are not, but without a strong correlation to one particular water mass (Reilly, 1990). One open question involves the stock identity of *D. delphis* seen farther west than 110°W in the central stock area, which are much closer to other sightings of *D. delphis* in the north stock area than they are to other sightings in the central stock area (Fig. 5). However, the central stock includes that offshore region because *D. delphis* in that region were bigger animals than those in the northern stock area, as were other *D. delphis* in the central stock area (Perrin *et al.*, 1985).

*Lagenodelphis hosei* has only recently been observed and recognized at sea, and earlier work speculated that its distribution in the eastern tropical Pacific would be similar to that of *Stenella longirostris* (Leatherwood *et al.*, 1988). All 33 sightings of *L. hosei* (25 used in the abundance estimate and eight 'off-effort') were south of 7°N (Fig. 6), and most were west of 100°W, far offshore, although there are other records of its occurrence in other parts of the ETP (Perrin *et al.*, In press). Therefore, the distribution of *L. hosei*, which is thought to be pantropical (Perrin *et al.*, In press), appears substantially different from the distribution of *S. longirostris* in the ETP (Fig. 3). Additionally, *L. hosei* appears to have an association with *Peponcephala electra*, as six of 18 sightings of *P. electra* were schools in which *L. hosei* and *P. electra* were found together. However, *P. electra* was also seen alone several times within the Gulf of Panama (Fig. 6) where *L. hosei* was absent, indicating *P. electra* are not restricted to equatorial waters, as previously thought (Au and Perryman, 1985). The association between *L. hosei* and *P. electra* has also been noted in other parts of the world (Perryman *et al.*, In press). *Lagenorhynchus obliquidens*, which occurs throughout much of the North Pacific (Leatherwood *et al.*, 1988), was seen only at the northern extreme of the study area (Fig. 6).

The three other small delphinids were found throughout most of the ETP. *Tursiops truncatus* was seen more frequently close to shore but was widespread in the ETP except offshore along 5°N latitude (Fig. 7), which suggests the offshore population may be divided into two populations, one north and one south of that parallel. *Grampus griseus* was seen most frequently in the shelf waters off Mexico and Guatemala, in the Gulf of Panama, and in the Peru current (Fig. 8). *Steno bredanensis* was seen at low densities everywhere except in the coldest parts of the Peru and California currents, where it was absent, with the most sightings in the warmest water close to the Mexican coast (Fig. 9), confirming its affinity for warm, tropical waters (Leatherwood *et al.*, 1988).

*Globicephala* sp. (probably all *G. macrorhynchus*, or nearly so, as discussed above) were most abundant in cold, upwelling-modified waters, and were absent from the warmest tropical waters off the Mexican coast (Fig. 10). There was a clear separation between short-finned pilot whales seen south of 15°N and those seen off the coast of Baja, Mexico (Fig. 10). These are likely to be separate stocks, and it is possible that the two populations represent two different forms in an analogous way to the cold-water and warm-water forms of short-finned pilot whales found in the western Pacific near Japan (Kasuya *et al.*, 1988). *Orcinus orca* was seen at low densities throughout the ETP, as were *Pseudorca crassidens* and *Feresa attenuata* (Fig. 11). However, more *P. crassidens* sightings were far offshore, while more *F. attenuata* sightings were close to the coast in the warmest water (Fig. 11). These patterns fit with what was known of their distributions (Leatherwood *et al.*, 1988).

Ziphius cavirostris was relatively abundant and found throughout the ETP (Fig. 12). Three sightings of *Mesoplodon peruvianus*, described from stranded animals in Peru (Reyes *et al.*, 1991) were seen, two off Peru and one off Mexico (Fig. 13). This agrees with the recent account of the first record of this species in the North Pacific, on the coast of Mexico (Urbán-Ramírez and Aurioles-Gamboa, 1992). *M. densirostris* was confirmed to have a fairly pelagic distribution (Leatherwood *et al.*, 1988), and appears to be distributed mostly in the southern portion of the ETP, as all 16 sightings of *M. densirostris* were south of 10°N (Fig. 13). Most of the 25 sightings of *Mesoplodon* sp. 'A' were off Mexico, although it was also seen off Central and South America, but not far offshore (Fig. 13). *Hyperoodon* sp. cf *H. planifrons*, previously described as having a population along the equator in the central Pacific (Leatherwood *et al.*, 1988), was seen only at 2°, 4°, 5° and 15°N, extending the known northern limit for this whale in the Pacific (Fig. 14). *Berardius bairdii*, which has a more northerly distribution (Leatherwood *et al.*, 1988), was only seen along the coast of Baja California, Mexico (Fig. 14).

*Physeter macrocephalus* was found throughout the ETP, but appeared to be most abundant in the Gulf of Panama (Fig. 15), formerly one of the primary sperm whaling grounds in the eastern Pacific (Leatherwood *et al.*, 1988). *Kogia simus* was also found throughout the ETP, but was seen most frequently near the coast (Fig. 16). *Balaenoptera musculus*, as has been previously described, was found in colder, nutrient-rich water of the California and Peru currents and the Costa Rican Dome (Reilly and Thayer, 1990; Fig. 17). *Megaptera novaeangliae* was similarly seen in the California and Peru currents, but was not seen in the Costa Rican Dome area, although it was seen once in the Gulf of Panama and once along the coast of Guatemala (Fig. 17). *Balaenoptera edeni* was widespread in its distribution, but appeared to have a hiatus in distribution from north to south, as no sightings were made between 7° and 9°N (Fig. 18). This suggests the possibility that there may be two stocks of *B. edeni* in the ETP. *B. acutorostrata* was only seen in the California and Peru currents, while *B. physalus* was only seen once, north of the study area along the coast of Baja, Mexico (Fig. 17). The majority of the unidentified *Balaenoptera* sp. sightings were probably *B. edeni*, or possibly *B. musculus* in the regions where it was found (Fig. 19).

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## Legends for Figs. 2–5

Fig. 2. Sightings of the three spotted dolphin (*Stenella attenuata*) stocks, showing offshore spotted dolphins (squares); coastal spotted dolphins (pluses); and unidentified spotted dolphins in the coastal stock area (triangles). The dashed line represents the dividing line within the study area for assigning sightings to the offshore stocks, with all offshore spotted sightings to the north and east of the line assigned to the northeastern stock (northeast), and offshore sightings to the south and west of the line assigned to the western/southern stock (west/south). The coastal stock boundary is the solid line paralleling the coast 185km (100 n.miles) offshore.

Fig. 3. Sightings of the two spinner dolphin (*Stenella longirostris*) stocks, showing eastern spinner dolphins (open squares); whitebelly spinner dolphins (pluses); and unidentified spinner dolphins in the overlap area (filled triangles). Eastern refers to the area occupied by the eastern spinner dolphin, represented as a dotted line. Whitebelly refers to the area occupied by the whitebelly stock, represented as a dashed line. Overlap refers to the area of overlap between the eastern and whitebelly stock areas. Central Amer. refers to the stock area of the Central American spinner, in which there was little effort during the survey, and consequently no spinner dolphin sightings.

Fig. 4. Sightings of the striped dolphin, *Stenella coeruleoalba* (squares).

Fig. 5. Sightings of the three common dolphin (*Delphinus delphis*) stocks, showing shortbeak (or 'offshore') common dolphins (open squares); longbeak (or 'Baja neritic') common dolphins (open circles); and unidentified common dolphins (pluses). The two dashed lines represent the dividing lines within the study area for assigning common dolphin sightings to stocks. All sightings in the north area were assigned to the northern stock, in the central area to the central stock, and in the south area to the southern stock. Note that two morphological types, shortbeak and longbeak, are both in the northern stock (see text for explanation).

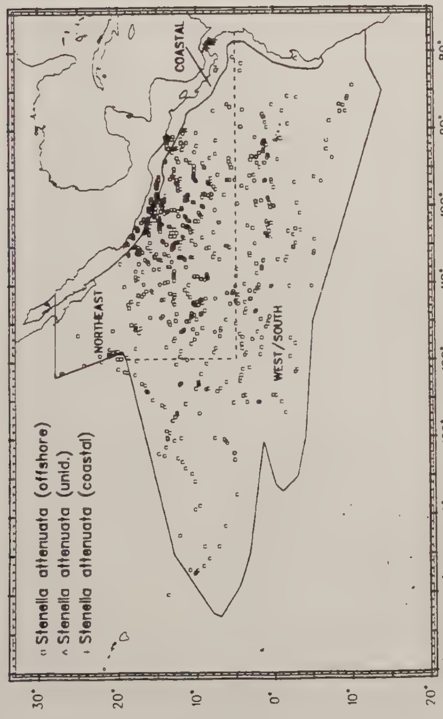
Stenella attenuata (offshore)
Stenella attenuata (unid.)
Stenella attenuata (coastal)
NORTHEAST
COASTAL
WEST/SOUTH
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 2.

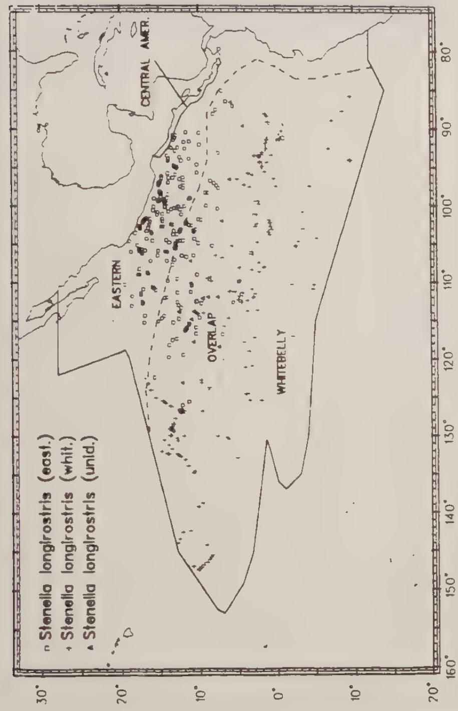
Stenella longirostris (east.)
Stenella longirostris (whit.)
Stenella longirostris (unid.)
CENTRAL AMER.
EASTERN
OVERLAP
WHITEBELLY
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 3.

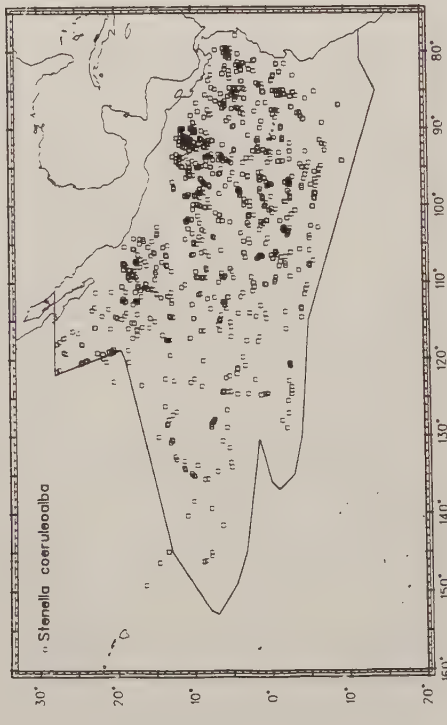
Stenella coeruleoalba
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 4.

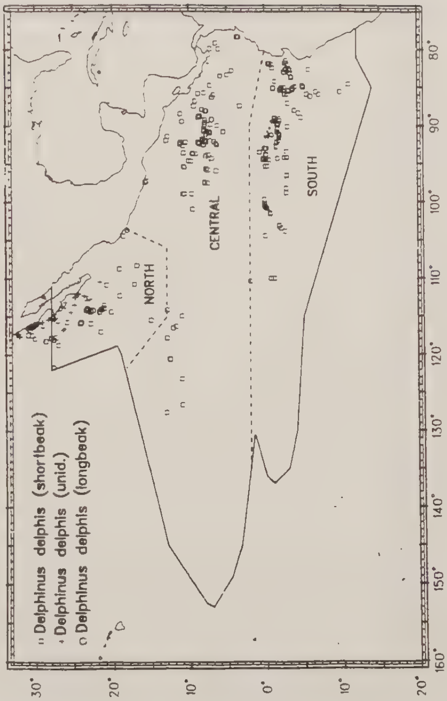
Delphinus delphis (shortbeak)
Delphinus delphis (unid.)
Delphinus delphis (longbeak)
NORTH
CENTRAL
SOUTH
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 5.

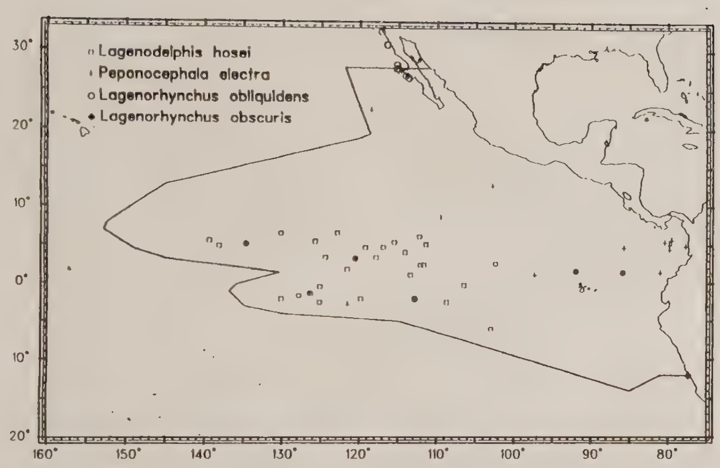
▫ Lagenodelphis hosei
+ Peponocephala electra
○ Lagenorhynchus obliquidens
◆ Lagenorhynchus obscuris
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 6. Sightings of Fraser's dolphin, *Lagenodelphis hosei* (open squares); the melon-headed whale, *Peponocephala electra* (pluses); the Pacific white-sided dolphin, *Lagenorynchus obliquidens* (open circles); and the dusky dolphin, *Lagenorynchus obscurus* (filled diamond).

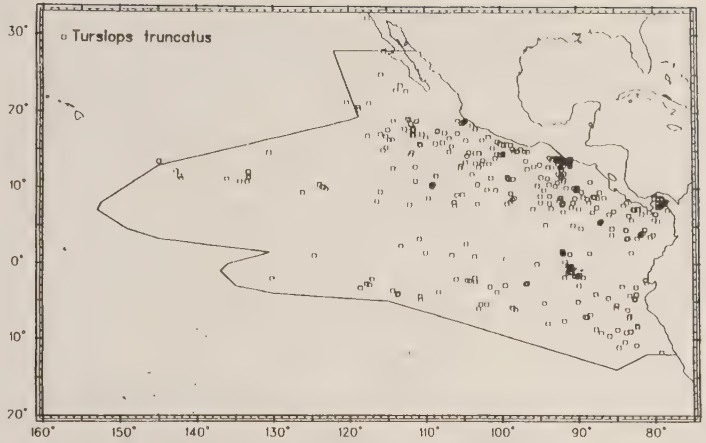
▫ Tursiops truncatus
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 7. Sightings of the bottlenose dolphin, *Tursiops truncatus* (squares).

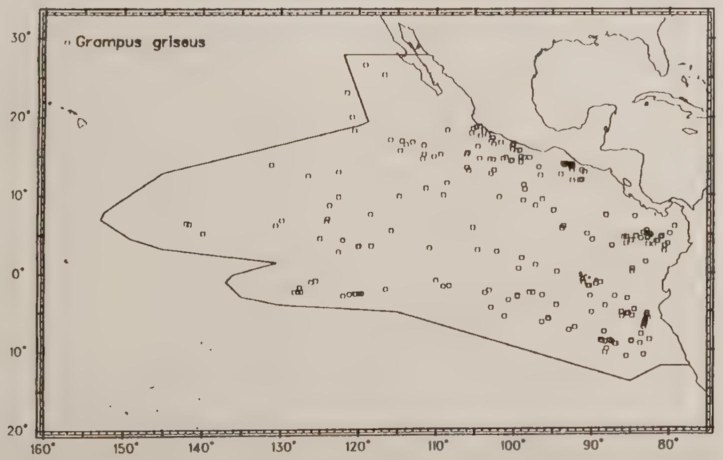
▫ Grampus griseus
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 8. Sightings of Risso's dolphin, *Grampus griseus* (squares).

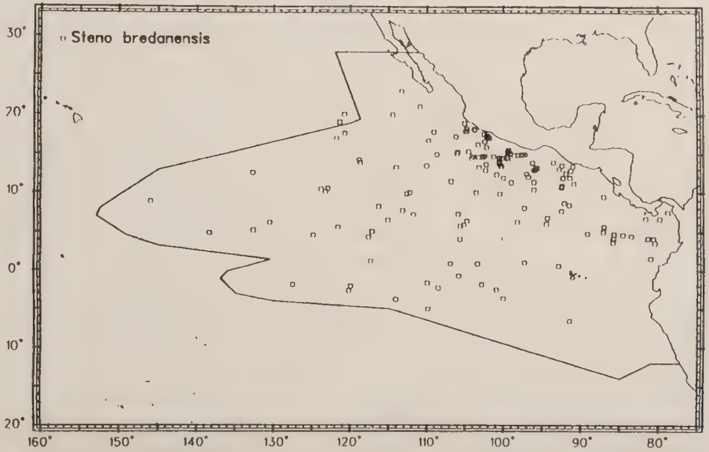
▫ Steno bredanensis
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 9. Sightings of the rough-toothed dolphin, *Steno bredanensis* (squares).

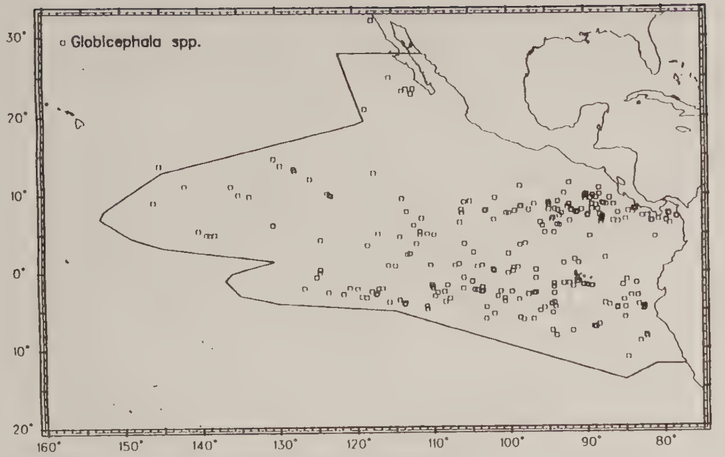
▫ Globicephala spp.
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 10. Sightings of pilot whales, *Globicephala* sp. (squares).

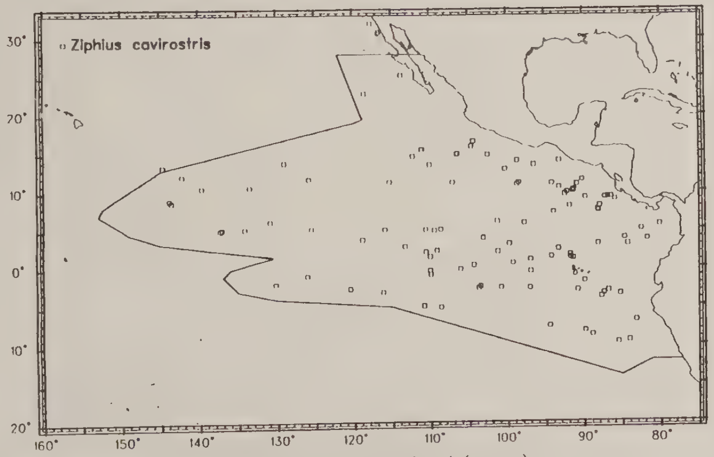
▫ Ziphius cavirostris
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 12. Sightings of Cuvier's beaked whale, *Ziphius cavirostris* (squares).

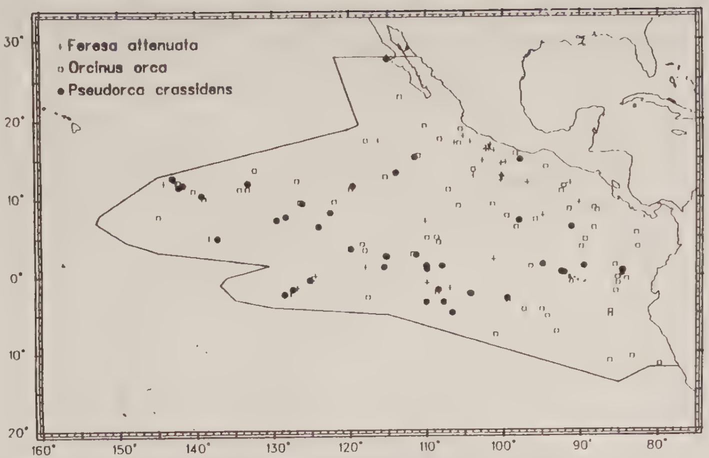
+ Feresa attenuata
▫ Orcinus orca
● Pseudorca crassidens
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 11. Sightings of the pygmy killer whale, *Feresa attenuata* (pluses); the killer whale, *Orcinus orca* (squares); and the false killer whale, *Pseudorca crassidens* (filled circles).

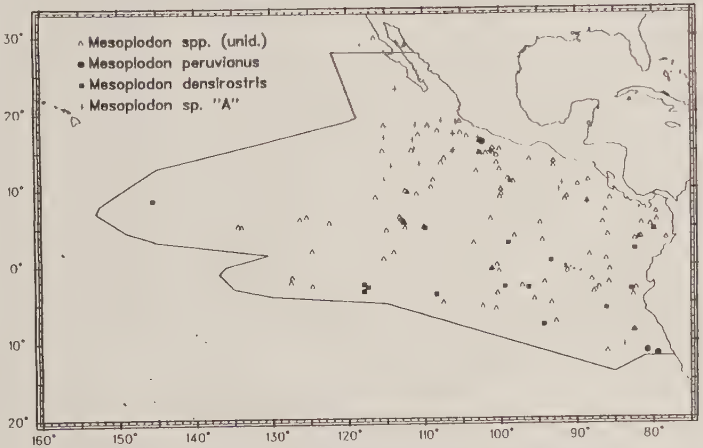
^ Mesoplodon spp. (unid.)
● Mesoplodon peruvianus
▪ Mesoplodon densirostris
+ Mesoplodon sp. "A"
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 13. Sightings of unidentified beaked whales, *Mesoplodon* sp. (open triangle); the pygmy beaked whale, *Mesoplodon peruvianus* (filled circles); Blainville's beaked whale, *Mesoplodon densirostris* (filled squares); and a possible new *Mesoplodon* sp. (Pitman *et al.*, 1987), called here sp. 'A' (pluses).

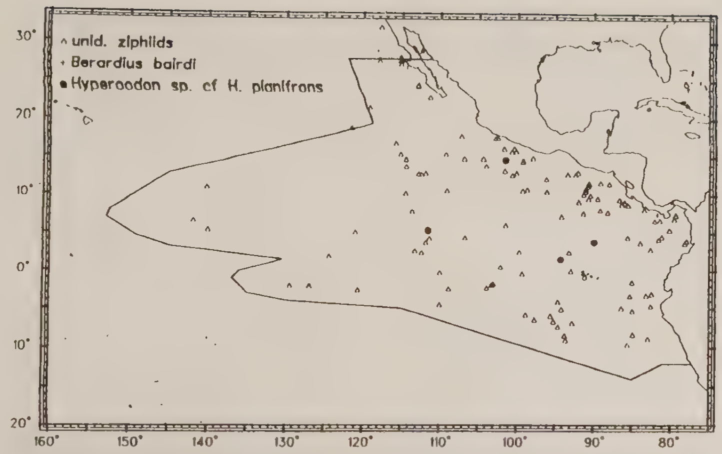
unid. ziphiids
Berardius bairdi
Hyperoodon sp. cf H. planifrons
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 14. Sightings of unidentified beaked whales, (ziphiids) (open triangles); Baird's beaked whale, *Berardius bairdi* (pluses), and a bottlenose whale, *Hyperoodon* sp. cf *H. planifrons* (filled circles).

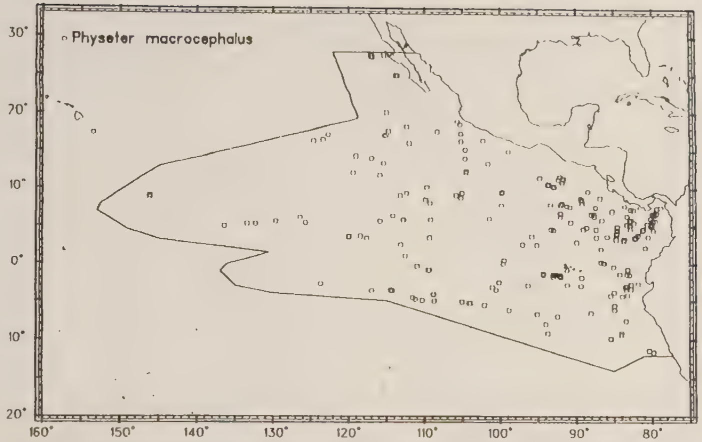
Physeter macrocephalus
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 15. Sightings of the sperm whale, *Physeter macrocephalus* (squares).

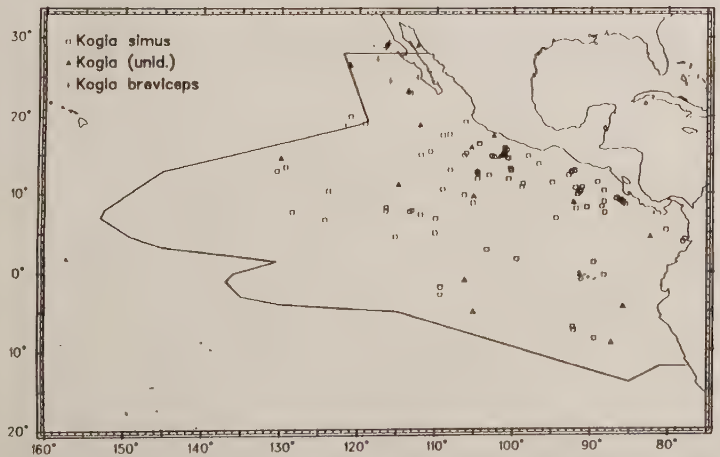
Kogia simus
Kogia (unid.)
Kogia breviceps
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 16. Sightings of the dwarf sperm whale, *Kogia simus* (open squares); the pygmy sperm whale, *Kogia breviceps* (pluses); and unidentified *Kogia* (filled triangles).

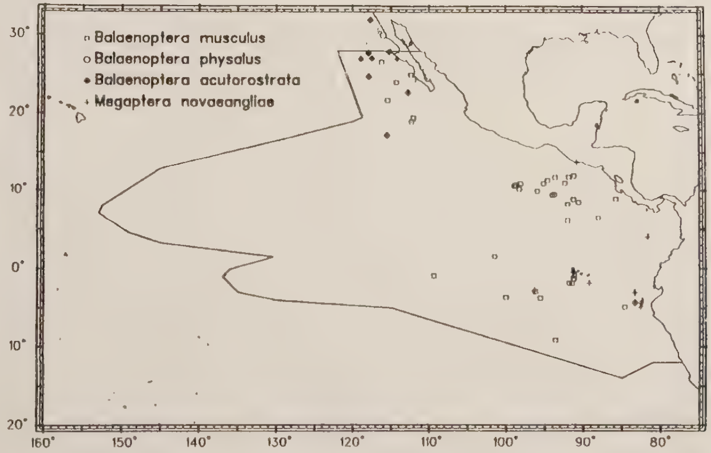
Balaenoptera musculus
Balaenoptera physalus
Balaenoptera acutorostrata
Megaptera novaeangliae
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 17. Sightings of the blue whale, *Balaenoptera musculus* (open squares); the fin whale, *Balaenoptera physalus* (open circle); the minke whale, *Balaenoptera acutorostrata* (filled diamonds); and the humpback whale, *Megaptera novaeangliae* (pluses).

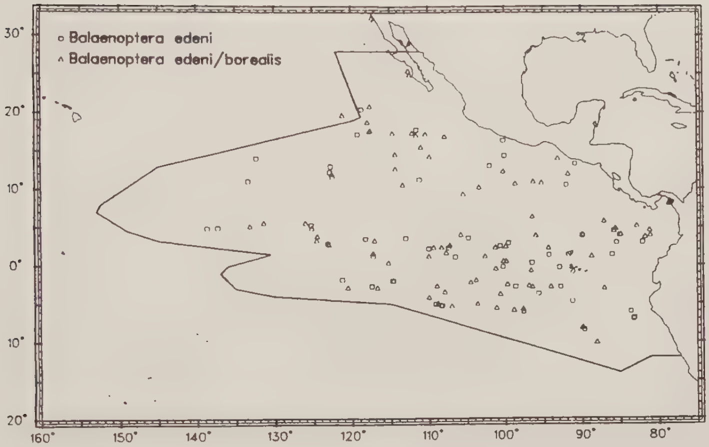
○ Balaenoptera edeni
△ Balaenoptera edeni/borealis
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 18. Sightings of Bryde's whale, *Balaenoptera edeni* (open squares) and rorquals identified as either a Bryde's or a sei whale, *Balaenoptera edeni/borealis* (open triangles; see text for explanation).

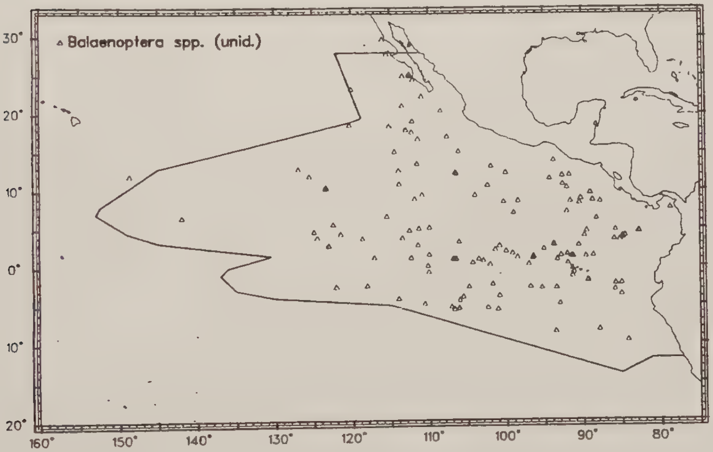
△ Balaenoptera spp. (unid.)
30°
20°
10°
0°
10°
20°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 19. Sightings of unidentified rorquals, *Balaenoptera* sp (triangles).

## ERRATA

For reasons outside our control, a number of errors found their way into paper SC/44/O 18.

p.478 **Data selection** Delete contents of bracket at end of 2nd sentence
p.478 **Stocks estimated** Last line, for 'Balaenoptera' read 'Balaenopteridae'
p.479 *Subfamily* **Globicephalinae**, for *Globicephala* sp. read *Globicephala* spp., throughout
p.479 *Family* **Ziphiidae**, for *Mesoplodon* sp. read *Mesoplodon* spp. throughout
p.480 Equation 2 should read

$$N_{jk} = \frac{n_{jk} f_{jk}(0)}{2L_k} \quad s_{jk} A_k$$

p.481 (2) *Unidentified spinner dolphins*, line 5, for 'with' read 'within'
p.481 (5) *Unidentified Balaenopteridae* (rorquals), line 4, for 'six' read 'five'; line 21, for '44' read '43'
p.482 2nd column, 2nd para. add reference to Table 3
p.483 Table 2 legend $N_j^*U$ and $N_j^*L$ should read $N_{jU}^*$ and $N_{jL}^*$
p.487 line 19 for 'Baja, Mexico' read 'Baja, California, Mexico', throughout
p.487 Reference to Gerodette and Perrin, 1991, delete *Deep-Sea Res.* 39:199-219
p.488 Delete reference to Tobayama *et al.* 1992.

9393

# Bycatch of Marine Turtles in North Pacific High-Seas Driftnet Fisheries and Impacts on the Stocks

by

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## I. ABSTRACT

Four species of marine turtles, all listed as threatened or endangered by the IUCN, have been documented in the bycatch of North Pacific high-seas driftnet fisheries. Bycatch rate data collected by observers, combined with driftnet fleet effort data, indicate a total marine turtle bycatch of about 6,100 turtles in 1990. The overall minimum marine turtle mortality due to driftnet entanglement in 1990 was about 1,700 turtles. Most of the mortalities were of loggerheads taken in the large-mesh driftnet fisheries of Japan and Taiwan. A reliable assessment of driftnet fishery impacts is hampered by lack of essential data on marine turtle population status and dynamics.

## II. INTRODUCTION

At least four species of marine turtles are caught incidentally and killed in North Pacific high-seas driftnet fisheries conducted by Japan, the Republic of Korea, and Taiwan. Because all marine turtle populations in the Pacific, and worldwide, are considered to be endangered or vulnerable, any mortality due to incidental entanglement in driftnets is cause for concern. Large-scale driftnet fishing may impact marine turtle populations by increasing mortality on juvenile, subadult, and adult turtles. The risk of mortality in driftnets is greatest for species which spend much of their lives in the open sea, such as leatherbacks and loggerheads. Assessing the impacts quantitatively and reliably, however, is difficult because essential data on population size and age structure are lacking.

The purpose of this paper is to summarize available information on the affected turtle populations and to discuss data bearing on the assessment of driftnet fishery impacts. We begin by reviewing information on the biology, life history, and distribution of the North Pacific marine turtle species encountered to date in the driftnet fisheries. We summarize data collected by scientific observers from the United States, Japan, Taiwan, Canada, and Korea as part of recent cooperative monitoring programs on the high-seas driftnet vessels. These data provide insights on many aspects of the pelagic distribution and ecology of marine turtles in the area of the driftnet fisheries that were totally unknown previously. We then review preliminary estimates of the magnitude of the mortality inflicted on marine turtle populations by driftnet fishing, again using data collected recently in the cooperative observer programs and additional information provided by the governments of Japan, Taiwan, and Korea. Finally, we discuss the difficulties of assessing population impacts given the high degree of uncertainty about the actual state of the populations and their dynamics.

## III. SPECIES AND POPULATIONS AFFECTED

Four species of marine turtles have been positively identified in the bycatch of the high-seas driftnet fisheries. These are the leatherback (*Dermochelys coriacea*), the loggerhead (*Caretta caretta*), the green turtle (*Chelonia mydas*), and the hawksbill (*Eretmochelys imbricata*). Although some observers have recorded the bycatch of the olive ridley (*Lepidochelys olivacea*) in monitored net sections, their identifications have been shown to be either incorrect or inconclusive.

### 1. Leatherback Turtle

The leatherback is the most distinctive and easily recognizable of the seven extant species of marine turtles. This is due to its large adult size, presence of seven longitudinal dorsal ridges, and absence of any cornified epidermal scutes, scales, or claws found in the hardshelled species of marine turtles. The leatherback is black with white speckling on the dorsal surfaces, and whitish on the ventral surfaces where five longitudinal ridges occur. The overall body has been described as deep and somewhat barrel-shaped, having a continuous covering of tough rubbery skin (Pritchard 1971, 1979; Pritchard and Trebbau 1984; Groombridge 1982). With a verified maximum weight of over 910 kg, the leatherback is the largest living turtle. It is the sole species included in the family Dermochelyidae; all other species of marine turtles are in the family Cheloniidae, the so-called "hard-shelled" turtles. The front flippers are disproportionately long compared to other marine turtles, making the leatherback a powerful swimmer in the open seas that it inhabits.

Leatherbacks, along with the olive ridley turtle, are ecologically unique among marine turtles by leading a completely pelagic existence throughout life, except during nesting. Like all marine turtles, the adult females must periodically return to land to lay eggs. The early life stages of other marine turtles (hatchlings and juveniles up to 25-50 cm or more in carapace length (CL), depending on the species) all pass through a pelagic phase of development (Carr 1986a). Then, after several years or more, they recruit to coastal or reef areas and establish a benthic existence.

The leatherback's diet is also unique among marine turtles in that it consists almost entirely of jellyfish (Scyphomedusidae) and planktonic tunicates such as *Salps* and *Pyrosoma* (Thaliacea). Leatherbacks are known to be among the deepest diving of air-breathing vertebrates with depths of 1200 m having been documented (Eckert *et al.* 1986; Mrosovsky 1987). The reason for diving so deep has not been determined, but may be related to feeding, or possibly thermoregulation; a leatherback may need to cool itself while in tropical waters or following strenuous nesting on land.

The leatherback is a circumglobal species which nests on certain selected beaches located between 30°N and 20°S. Away from these beaches leatherbacks are highly migratory, covering great distances that involve intentional movements into temperate and cooler waters to forage. Measurements on a leatherback captured off Nova Scotia show that the species is capable of maintaining a body temperature of at least 18°C above ambient seawater of 7.5°C. As with all marine turtles, very little is known of leatherback ecology and life history when they inhabit the open seas. For example, post-hatchling and subadult leatherbacks are almost never encountered.

Leatherback populations found in pelagic regions of the North Pacific originate from, and return to reproduce, at distant nesting beaches of uncertain identity. A plausible nesting beach of origin for leatherbacks encountered by driftnet vessels fishing in the North Pacific Transition Zone would be Rantau Abang in Trengganu State on the east coast of peninsular Malaysia. During the past 30 years, the leatherback population at this world-famous nesting beach has declined from an estimated 1,000-2,000 females nesting annually, to about 30-50 nesting females during the 1989 season (Mortimer 1990; see also Siow and Moll 1982). Leatherback nesting sites south of the equator in Irian Jaya (Indonesia) may also contribute to pelagic populations in the North Pacific, although much less is known about them.

Leatherbacks occurring off Japan (Nishimura 1964) very likely originate from one or both of these nesting areas in southeast Asia. The leatherback's penetration eastward into the North Pacific could be easily facilitated by (but not necessarily require) the Kuroshio Extension current. Leatherback nesting of any magnitude elsewhere in the Pacific occurs only along the Americas. Major nesting beaches occur from Michoacan south to Oaxaca, in Mexico, and in northern Costa Rica (Pritchard 1982; Pritchard and Trebbau 1984). Leatherbacks from these eastern Pacific nesting beaches may also contribute to pelagic populations encountered by driftnets in the North Pacific, since the species is commonly seen in higher latitudes of the eastern North Pacific off Canada and the U.S. The leatherback nesting population on the Pacific coast of Mexico is probably the largest in the world, numbering thousands of females annually, but its current conservation status is unclear.

## 2. Loggerhead Turtle

The loggerhead is a hardshelled marine turtle with an elongated reddish-brown carapace having five vertebral scutes and five (but sometimes only four) pairs of costal scutes. The plastron and other ventral surfaces are yellowish-white to yellowish-brown. The head, which has two pairs of prefrontal scales, is large, broad, and triangular with powerful jaws. Adults have a smooth carapace measuring 70-90 cm in length at the onset of sexual maturity. The maximum adult size of the loggerhead rarely exceeds 100 cm CL. In juveniles up to 35-50 cm CL the carapace has projections or elevated knobs toward the posterior of each vertebral scute and, to a lesser degree, each costal scute (Dodd 1988; Groombridge 1982; Pritchard 1979; Pritchard and Trebbau 1984).

The loggerhead is a circumglobal species found in temperate and subtropical waters. Nearly all nesting (except for the Western Caribbean) takes place north of 25°N or south of 25°S. Adult loggerheads undertake lengthy reproductive migrations to and from their historical nesting sites, but dispersal patterns in foraging areas are not well known for any population.

As with other marine turtles, hatchling loggerheads rapidly depart from their natal beaches and enter into a pelagic and planktonic stage of development where they are only rarely located and studied. The time spent in the open ocean is believed to last for at least three, and very likely five or more years. Research conducted by Carr (1986a, 1986b), and more recently by Bolten and Bjorndal (1991), has shown that some young Atlantic loggerheads feed at the surface over deep water near the Azores, where convergences and downwelling concentrate available food such as coelenterates and other planktonic invertebrates. The loggerheads in this pelagic region almost certainly originate from major nesting beaches in the Southeastern United States. Passive drift in the Gulf Stream and North Atlantic Gyre, in combination perhaps with periods of residency in smaller local ocean gyres, has been proposed to account for the turtles' hypothesized eventual return to the Americas. Upon returning, at a size exceeding 50-60 cm CL, recruitment to benthic habitats takes place. As benthic dwellers at this larger size loggerheads continue to be carnivorous, but now feeding primarily on molluscs and crustaceans.

In the North Pacific, where until recently even less was known about the ecological geography of immature loggerheads, the only major nesting beaches are in the southern part of Japan along the east and west coasts of Kyushu, the southeast coast of Shikoku, and the southeast and northeast coasts of Honshu (Nishimura 1967; Uchida and Nishiwaki 1982; Dodd 1988). Although reliable counts are not available, as many as 2,000-3,000 loggerheads may nest annually on beaches throughout Japan.

In the temperate zone of the South Pacific, loggerhead nesting is widespread and abundant in Queensland and western Australia, where in excess of 3,000 females are estimated to nest annually (Limpus 1982). In the Eastern Pacific, along the Americas, as well as in the central Pacific, nesting loggerheads are virtually nonexistent. However, large numbers of subadult loggerheads have been reported over deep water 42 km off the Baja California coast of Mexico (Dodd 1988; Balazs 1989; Bartlett 1989). In southern Mexico and Pacific Central America, loggerheads are exceedingly rare, if in fact they occur there at all. The origin of young loggerheads off Baja California is therefore an enigma in need of investigation. The possibility exists that these turtles may be part of the Japanese population. Some support for this hypothesis has been provided by Uchida and Teruya (1991) in reporting the recovery of a tagged loggerhead found 75 km off San Diego (Southern California) that had been released 2.3 years earlier off Okinawa at a size of 17.5 cm carapace length.

Immature loggerheads encountered during driftnet fishing in the North Pacific most probably originate from nesting beaches in Japan, being transported to the north and east by the Kuroshio and its extension. The apparent similarities of young loggerheads reported off Baja California to the circumstances off the Azores, raises the possibility of pelagic Pacific-wide migrations by the Japanese loggerheads. Additional research will be needed to confirm or reject this hypothesis.

### 3. Green Turtle

The green turtle is a hard-shelled marine turtle with a smooth heart-shaped carapace having five vertebral scutes and four pairs of costal scutes. The head is relatively small and anteriorly rounded with a single pair of elongated prefrontal scales. The coloration of the carapace in adult green turtles, as well as immature size classes, varies considerably, ranging from black to brown, olive, yellow and combinations thereof. The plastron and other ventral surfaces range from pure white in the juvenile to yellowish and orange in the adult. However, green turtles that nest on the Pacific coast of Mexico, often referred to as the "black turtle", are distinguished by their heavy black dorsal pigmentation, a highly arched carapace, small size at the onset of sexual maturity (70 cm CL compared to >82 cm CL elsewhere), and considerable grey or black pigment in the plastron (Hirth 1971; Pritchard 1979; Pritchard and Trebbau 1984; Groombridge 1982).

The green turtle's lower jaw-edge is coarsely serrated corresponding to strong grooves and ridges on the inner surface of the upper jaw. This generic feature relates to the fact that green turtles are the only marine turtle with a nearly exclusive herbivorous diet (e.g. sea grass and algae) following their recruitment into shallow benthic habitats from the pelagic phase of development. Nutritional limitations of herbivory (Bjorndal 1982) result in green turtles exhibiting generally slow rates of growth and a delayed sexual maturity estimated to be 15-50 years in the wild. The average adult size of the green turtle varies between nesting sites (e.g. 92 cm in Hawaii, 105 cm in Surinam) where migrations are periodically undertaken and nesting females show a strong fidelity throughout their reproductive life.

The green turtle is a circumglobal and highly migratory species nesting mainly in tropical and subtropical regions. It inhabits waters that usually remain above 20°C in the coldest month. Like other marine turtles, the species should not be regarded as a single interbreeding assemblage, but rather as a complex of populations, or stock units, having geographically discrete nesting sites. These breeding populations have little, if any, ability to demographically reinforce one another. Once a population has been depleted, there is no evidence that it can be restored over foreseeable time by turtles originating from other populations.

Approximately 150 separate nesting colonies for the green turtle are known worldwide, however only about 10-15 of these are considered large enough to involve 2,000 or more nesting females per year (Groombridge 1982). In the Pacific, major populations are restricted to Australia, Mexico, and Malaysia. Small, and in many cases reduced, nesting colonies of green turtles are scattered throughout the insular Pacific islands of Polynesia, Micronesia, and Melanesia (Forsyth and Balazs 1989).

Green turtles encountered during driftnet fishing in the North Pacific may originate from a number of known proximal, or even distant, breeding colonies in the region. However, the most likely candidates would include French Frigate Shoals in the Hawaiian Islands (Balazs 1980; Balazs *et al.* 1990) and the Ryukyu and Ogasawara Islands of Japan (Suganuma 1985; Uchida and Nishiwaki 1982).

### 4. Hawksbill Turtle

The hawksbill turtle is a hardshelled marine turtle distinguished by its narrow head, tapering beak, thick overlapping scutes (known in commerce as "tortoiseshell" or "bekko"), and a strongly serrated margin to the carapace. The head has two pairs of prefrontal scales, while the carapace has five vertebral scutes and four pairs of costal scutes. There are highly variable colour patterns to the carapace ranging from clear amber to brown to black. The plastron in the adult is usually pure yellow or orange-yellow, while juveniles frequently have large black spots on the plastron. Mean carapace lengths of adult female hawksbills range from 66 cm to 86 cm worldwide (Witzell 1983; Pritchard and Trebbau 1984; Groombridge 1982).

The hawksbill occurs circumglobally and is the most tropical of all marine turtles. Nesting is widespread, but sparse, in tropical regions worldwide; large nesting colonies are atypical. In benthic habitats, following an unknown developmental period spent on the high-seas, hawksbills forage principally on sponges. In the Pacific, with the exception of Australia, nesting does not occur in abundance (Groombridge and Luxmoore 1989). The hawksbill is commonly considered one of the most endangered species of marine turtles due to the long history of international commercial trade in tortoiseshell.

Hawksbills encountered in the North Pacific high-seas driftnet fisheries may originate from the proximal, albeit low level, nesting sites to the southwest in the Hawaiian Islands (see Balazs *et al.* 1990). An alternate, or additional, origin may be beaches in the south of Japan, including the Ryuku Islands and Okinawa, where hawksbill nesting occurs as a rare event (Uchida and Nishiwaki 1982; Kamezaki 1987; Teruya and Uchida 1988).

## IV. SOURCES OF MARINE TURTLE MORTALITY

Marine turtles have been adversely affected by an array of human-induced factors that have resulted in the species being designated as threatened and endangered. Declines in marine turtles have brought them under restrictive, but by no means fully effective, international trade agreements by consenting nations (CSTC 1990, Groombridge and Luxmoore 1989).

All marine turtle life stages are susceptible to human-induced mortality. On nesting beaches direct exploitation of turtles for meat, eggs, hides, and other products takes place for both commercial markets and local utilization. For example, in Kagoshima Prefecture, Japan, loggerhead eggs are taken for local consumption, and fishermen often take the adults to eat whenever encountered in the nearshore waters (Deguchi 1991). In the Ogasawara Islands, green turtles are hunted for food by the local inhabitants, and subadults are commonly caught and drowned in monofilament fishing nets (Suganuma 1991). Likewise, in the Hawaiian Islands green turtles were historically harvested by the indigenous population, and later by European settlers. Although protected now by Hawaii state and U.S. Federal laws, they are frequently killed in inshore gillnets targeting fish.

On nesting beaches and in nearshore waters, habitat degradation and destruction have occurred from such diverse factors as coastal development, dredging, vessel traffic, erosion control, sand mining, vehicular traffic on beaches, and artificial lighting that repels the adults and disorients the hatchlings. Human alteration of terrestrial habitats can also change the feeding patterns of natural predators, thereby increasing predation on marine turtle nests and eggs.

Petroleum and other forms of chemical pollution affect turtles throughout their marine and terrestrial habitats. Direct poisoning, as well as blockage of the gastrointestinal tract by ingested tar balls, has been reported. Low level chemical pollution possibly causing immunosuppression has been suggested as one factor in the epidemic outbreak of a tumour disease in green turtles (Balazs and Pooley 1991). Plastics and other persistent buoyant debris discharged into the ocean are now also recognized as harmful pollutants, especially to juvenile and subadult turtles in the pelagic environment. Both the entanglement in, and ingestion of, this synthetic debris have been documented (Balazs 1985; Carr 1987).

The incidental capture and mortality of turtles has been documented in various fisheries, including those using longlines, trawls, purse seines, and gillnets (Crouse 1984). In the North Pacific, the incidental take of leatherbacks in the high-seas driftnet fisheries was first reported by Balazs (1982a), who earlier (Balazs 1982c) had described the occurrence of leatherbacks in the region as reported to him by commercial fishermen. In the Eastern Tropical Pacific marine turtles are sometimes taken in tuna purse seines and throughout the Pacific they are occasionally hooked or entangled by tuna longline gear. Little quantitative information on such incidental capture has been available. Recently, however, Nishimura and Nakahigashi (1990) estimated that in the North Pacific and South China Sea approximately 21,200 turtles, including loggerheads and greens, were captured each year in tuna longlines and bottom trawls, with a reported mortality of 12,300 turtles per year. The estimates were based on turtle capture rates reported in a survey of fisheries research and training vessels and extrapolated to total longline fleet effort.

## V. STATUS OF MARINE TURTLE POPULATIONS

The leatherback is listed as endangered worldwide by the International Union for Conservation of Nature and Natural Resources (IUCN), and it appears on Appendix I (most restrictive category) of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). The species is also listed as endangered under the U.S. Endangered Species Act.

The loggerhead is listed as vulnerable worldwide by the IUCN, and it appears on Appendix I of CITES. The species is listed as threatened under the U.S. Endangered Species Act.

The green turtle is listed as endangered worldwide by the IUCN, and it appears on Appendix I of CITES. The species is listed as threatened under the U.S. Endangered Species Act, except for nesting populations in Florida and on the Pacific Coast of Mexico where they are listed as endangered.

The hawksbill is listed as endangered worldwide by the IUCN, and it appeared on Appendix I of CITES. It is also listed as endangered under the U.S. Endangered Species Act.

In the case of Pacific leatherbacks, hawksbills, and the Hawaiian green turtle, available data indicate that current populations are at much lower levels than those observed historically. Less appears to be known about Japanese loggerheads and green turtles.

Most available information on marine turtle stock size pertains to nesting females and is often piecemeal, qualitative and anecdotal. Because nesting females are accessible, however, it is relatively easy to survey nesting populations and estimate hatchling production. Assessment of juvenile and subadult abundance is much more difficult. In Hawaii the green turtle nesting colony at French Frigate Shoals has been assessed annually since 1973. Although there is considerable interannual variation in the estimates of nesting females, the trend appears to be upward, possibly a result of state and federal laws protecting turtles from exploitation. Tag-recapture methods are now being explored to estimate inshore populations of Hawaiian green turtles; no results are yet available. Models to determine likely population recovery rates are also under development.

Virtually nothing is known about the capacity of marine turtle populations to compensate for increased mortality through density-dependent changes in growth, maturation rate, remigration interval, clutch size, or other factors. Considerable variation in growth rates has been documented among tagged turtles in the wild, even within single populations (Balazs 1982b; Bjorndal and Bolten 1988a, 1988b). Observed growth rate variation may have genetic origins or be due to differences in ambient temperature or quality of forage. Conceivably, growth rates could also depend on the quantity of food available. While the latter possibility may suggest that density-dependent growth compensation is possible, such responses have not been demonstrated. Except on turtle nesting beaches, where nest superimposition has been observed and suggested as a mechanism of density dependence in hatchling production (e.g., Bustard and Tognetti 1969), comments about density-dependent compensation are speculative. Further, given the longevity and late maturation of marine turtles, population recovery is likely to be very protracted and decades may be required to rebuild depleted nesting populations unless mortality rates are reduced sharply in all age groups.

## VI. BYCATCH IN THE DRIFTNET FISHERIES

### 1. Species Composition and Bycatch Rates

In the first multinational observer program, the 1989 pilot program on Japanese squid driftnet vessels, 9 of the 22 marine turtles recorded in the bycatch were leatherbacks; the remainder were unidentified. More extensive data collected in the 1990 observer programs in the Japanese, Korean, and Taiwanese squid driftnet fleets, and the large-mesh driftnet fleets of Japan and Taiwan, have shown that the turtle bycatch species composition varies considerably between the fisheries (Table 1). In the June-December 1990 Japanese squid fishery, observers identified 77.1% of the 35 marine turtles seen in the monitored bycatch as leatherbacks and 2.9% as loggerheads; the other 20.0% were unidentified. In the 1990 observer programs on Korean and Taiwanese squid driftnet vessels the monitored bycatch (a combined total of 8 turtles) included leatherback, green, loggerhead, and unidentified turtles (not differentiated between leatherback and hard-shelled species.)

In the large-mesh fisheries of Japan and Taiwan the turtle species composition of the monitored bycatch appears to be quite different. In the observer program on Japanese large-mesh vessels, conducted between September 1990 and May 1991, the monitored bycatch of 289 turtles consisted of 50.2% loggerheads; 31.1% unspecified hard-shelled turtles, 10.4% greens; 5.2% unidentified turtles; 2.8% leatherbacks; and a single (0.3%) hawksbill (Table 1). The monitored bycatch on

Table 1. Species composition and average bycatch rates (number per million standardized tans or poks) of marine turtles in the 1990 squid driftnet fisheries of Japan, Korea, and Taiwan, the 1990 large-mesh driftnet fishery of Taiwan, and the 1990-1991 large-mesh driftnet fishery of Japan.

SQUID FISHERIES

| | Japan | | | Taiwan | | | Korea | | |
|---|---|---|---|---|---|---|---|---|---|
| Monitored effort (millions of tans or poks) | 2.28 | | | 0.17 | | | 0.67 | | |
| Species | Bycatch | CPUE | Percent | Bycatch | CPUE | Percent | Bycatch | CPUE | Percent |
| Leatherback | 27 | 11.8323 | 77.14 | 0 | 0.0000 | 0.00 | 2 | 2.9866 | 33.33 |
| Loggerhead | 1 | 0.4382 | 2.86 | 0 | 0.0000 | 0.00 | 0 | 0.0000 | 0.00 |
| Green | 0 | 0.0000 | 0.00 | 1 | 5.8680 | 50.00 | 1 | 1.4933 | 16.67 |
| Hawksbill | 0 | 0.0000 | 0.00 | 0 | 0.0000 | 0.00 | 0 | 0.0000 | 0.00 |
| Unspecified hard-shelled | 0 | 0.0000 | 0.00 | 1 | 5.8680 | 50.00 | 0 | 0.0000 | 0.00 |
| Unidentified | 7 | 3.0676 | 20.00 | 0 | 0.0000 | 0.00 | 3 | 4.4799 | 50.00 |
| TOTAL | 35 | 15.3381 | 100.00 | 2 | 11.7361 | 100.00 | 6 | 8.9597 | 100.00 |

LARGE-MESH FISHERIES

| | Japan | | | Taiwan | | |
|---|---|---|---|---|---|---|
| Monitored effort (millions of tans) | 0.51 | | | 0.19 | | |
| Species | Bycatch | CPUE | Percent | Bycatch | CPUE | Percent |
| Leatherback | 8 | 15.6375 | 2.77 | 8 | 41.0362 | 10.53 |
| Loggerhead | 145 | 283.4301 | 50.17 | 8 | 41.0362 | 10.53 |
| Green | 30 | 58.6407 | 10.38 | 0 | 0.0000 | 0.00 |
| Hawksbill | 1 | 1.9547 | 0.35 | 0 | 0.0000 | 0.00 |
| Unspecified hard-shelled | 90 | 175.9221 | 31.14 | 5 | 25.6476 | 6.58 |
| Unidentified | 15 | 29.3204 | 5.19 | 55 | 282.1236 | 72.37 |
| TOTAL | 289 | 564.9055 | 100.00 | 76 | 389.8435 | 100.00 |

Taiwanese large-mesh vessels included 76 marine turtles, of which 10.5% were leatherbacks, 10.5% were loggerheads, 6.6% were unspecified hard-shelled turtles, and 72.4% were completely unidentified.

In addition to the differences in species composition of the turtle bycatch, observer data indicate substantial differences in marine turtle bycatch rates between squid and large-mesh driftnet fisheries. In the Japanese squid driftnet fishery, 1990 observer data showed an aggregate bycatch rate of 15.3 turtles per million standardized tans (a standardized tan is defined as a 50 m length of driftnet.) In the 1990 Korean squid fishery, the turtle bycatch rate was 9.0 turtles per million standardized poks (equivalent to tans). The turtle bycatch rate was 11.7 turtles per million tans in the 1990 Taiwanese squid fishery.

In the large-mesh driftnet fishery the overall turtle bycatch rate was 564.9 turtles per million tans for Japan (1990-1991 season) and 389.8 turtles per million tans for Taiwan (1990 season). The ratio of turtle bycatch in the large-mesh driftnet fleet to the bycatch rate in the squid fleet was 33:1 for Taiwan, and 37:1 for Japan.

## 2. Turtle Size Composition

Information about the size distribution of marine turtles in waters fished by the high-seas driftnet fleets did not exist prior to the cooperative observer programs. Observer guidelines for all U.S. observers, and most other observers, called for them to measure the curved carapace length of each turtle encountered or, if accurate measurements were impossible, to estimate the carapace length. We do not yet have access to all turtle length data collected, but those available to us provide a preliminary assessment of length composition.

Estimates or measurements of leatherback carapace lengths ranged from 70 cm to about 300 cm, with most falling between 100 cm and 200 cm. Almost all leatherbacks dropped out of the nets during retrieval or were cut out before being decked, so lengths were simply estimated, often roughly. It is likely that many of the leatherbacks encountered were mature.

Loggerheads ranged from 12 cm to about 90 cm CL. There was a bimodal distribution, with most turtles falling between 40 cm and 80 cm, and a somewhat smaller cluster between 10 cm and 30 cm (Figure 1). Many loggerheads were decked and accurate measurements were made. Available data on growth rates and size at maturity suggest that the majority of loggerheads encountered were immature.

Green turtles ranged from 24 cm to 49 cm CL, and also showed a bimodal distribution, with one group shorter than 35 cm and a second group longer than 40 cm (Figure 1). All green turtles measured by observers were immature.

The single hawksbill recorded by an observer was 46 cm CL, and was immature.

## 3. Spatial Distribution of the Turtle Bycatch

The temporal and spatial variation in turtle bycatch rates and factors affecting them are still being studied and will be the subject of a later report (Balazs and Wetherall *in prep*). A preliminary analysis, however, shows that leatherbacks were taken over a wide range of longitudes, from 156°W to 150°E, and at latitudes from 31°N to 43°N. Loggerheads were also encountered over a wide area, from 154°W to 150°E, and from 28°N to 39°N. Green turtles were identified in the bycatch from 154°W to 154°E, and from 28°N to 37°N. The single hawksbill was encountered at 173°E and 29°N. These descriptions of distribution are based on the combined data from the 1989 and 1990 observer programs but mask any monthly variations, which we have not yet analyzed. Further, they indicate only the spatial distribution of turtle bycatch within the range of the monitored fishing effort, not the potential spatial distribution within the broader range of total fleet effort (Figures 2-5), or the potential spatial distribution of the turtles themselves.

## 4. Total Bycatch in the Squid Driftnet Fisheries

Estimates of total bycatch may be made by expanding the bycatch rate statistics by the total fishing effort exerted by the squid driftnet fleet. Some of the fleet effort data essential to the reliable estimation of bycatch levels are not yet available. Further, all estimates involve assumptions which may not be verifiable. In several instances the bycatch estimates discussed here are preliminary but should at least indicate the general magnitude of the bycatch.

In the 1989 Japanese squid driftnet fishery 22 turtles were counted by observers in 1.4 million monitored tans of fishing effort. Since the total fleet effort was 34.4 million tans, a simple expansion of the sample data provides a total bycatch estimate of 529 turtles. By dividing the data into time-area strata, Balazs and Wetherall (1991) estimated a total bycatch of 544 turtles, all species combined (95% confidence interval 360-742 turtles). If the 544 turtles are apportioned by the species composition of the monitored bycatch the results suggest a total bycatch of 222 leatherbacks and 322 unidentified turtles. Using the same data but different assumptions, Yatsu and Hayase (1991) estimated a total bycatch of 472 marine turtles including 221 leatherbacks and 251 other turtles.

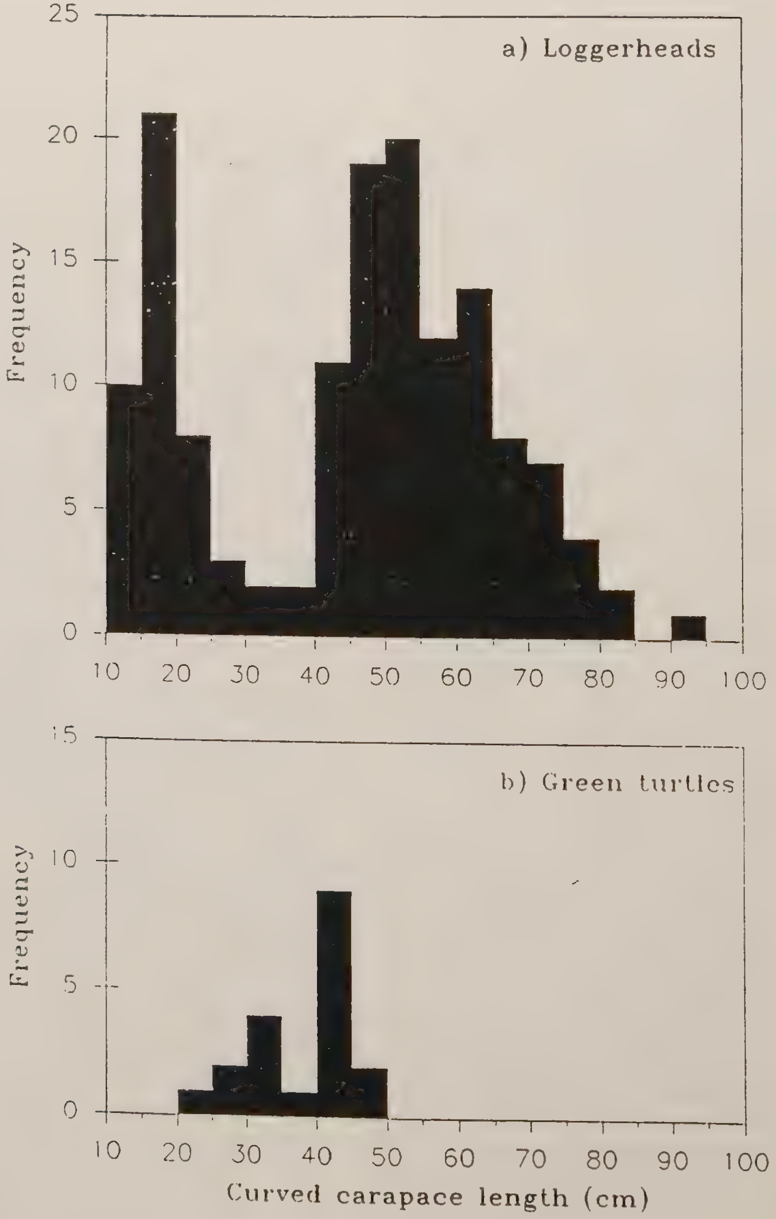

Fig. 1. Carapace length frequency distributions for (a) loggerheads and (b) green turtles encountered in North Pacific high-seas driftnet fisheries, based on U.S. observer data.

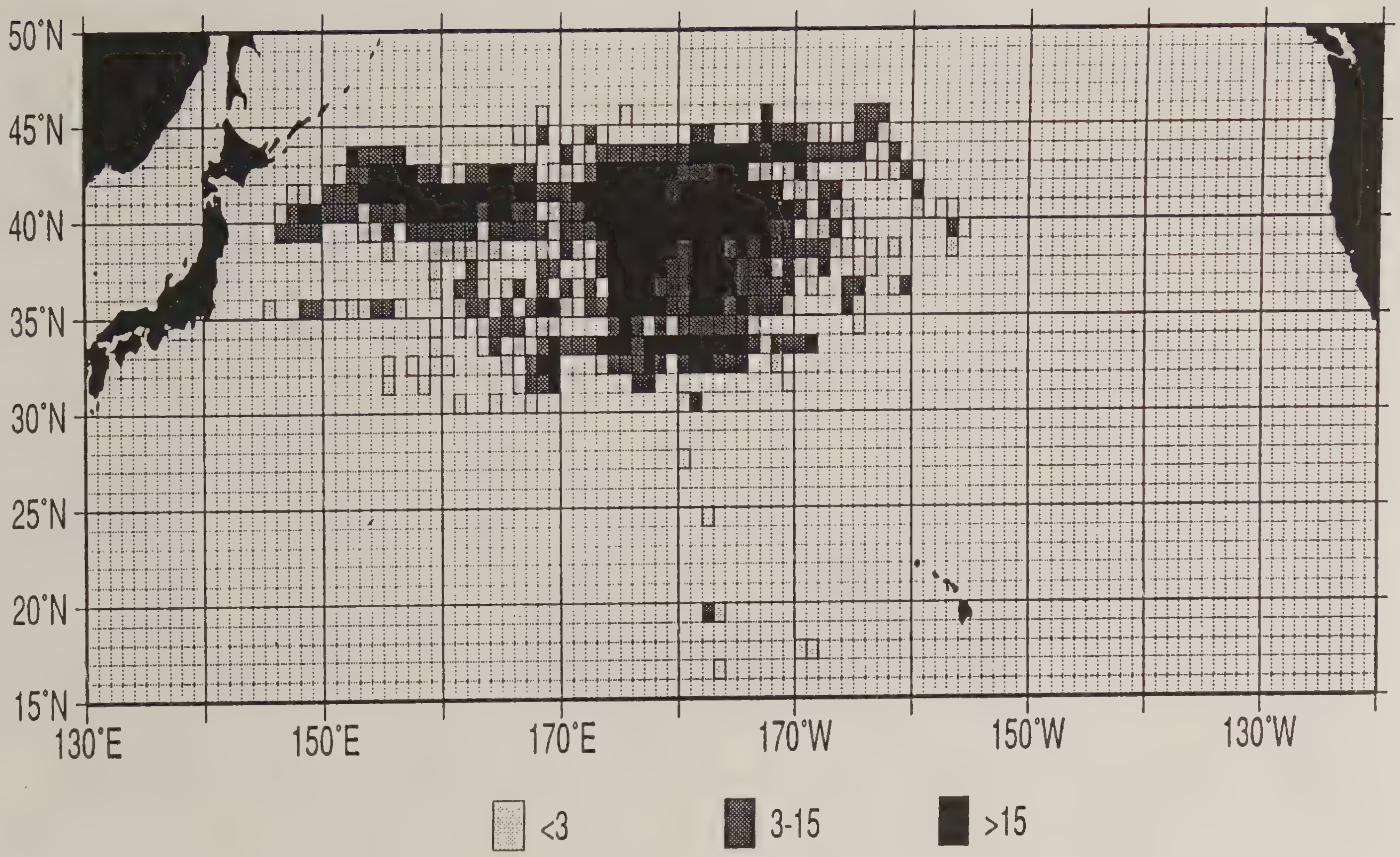
50°N
45°N
40°N
35°N
30°N
25°N
20°N
15°N
130°E
150°E
170°E
170°W
150°W
130°W
<3
3-15
>15

Fig. 2. Distribution of fishing effort in the 1990 Taiwanese North Pacific high-seas driftnet fishery (squid and large-mesh gear combined). Units are vessel-days of fishing.

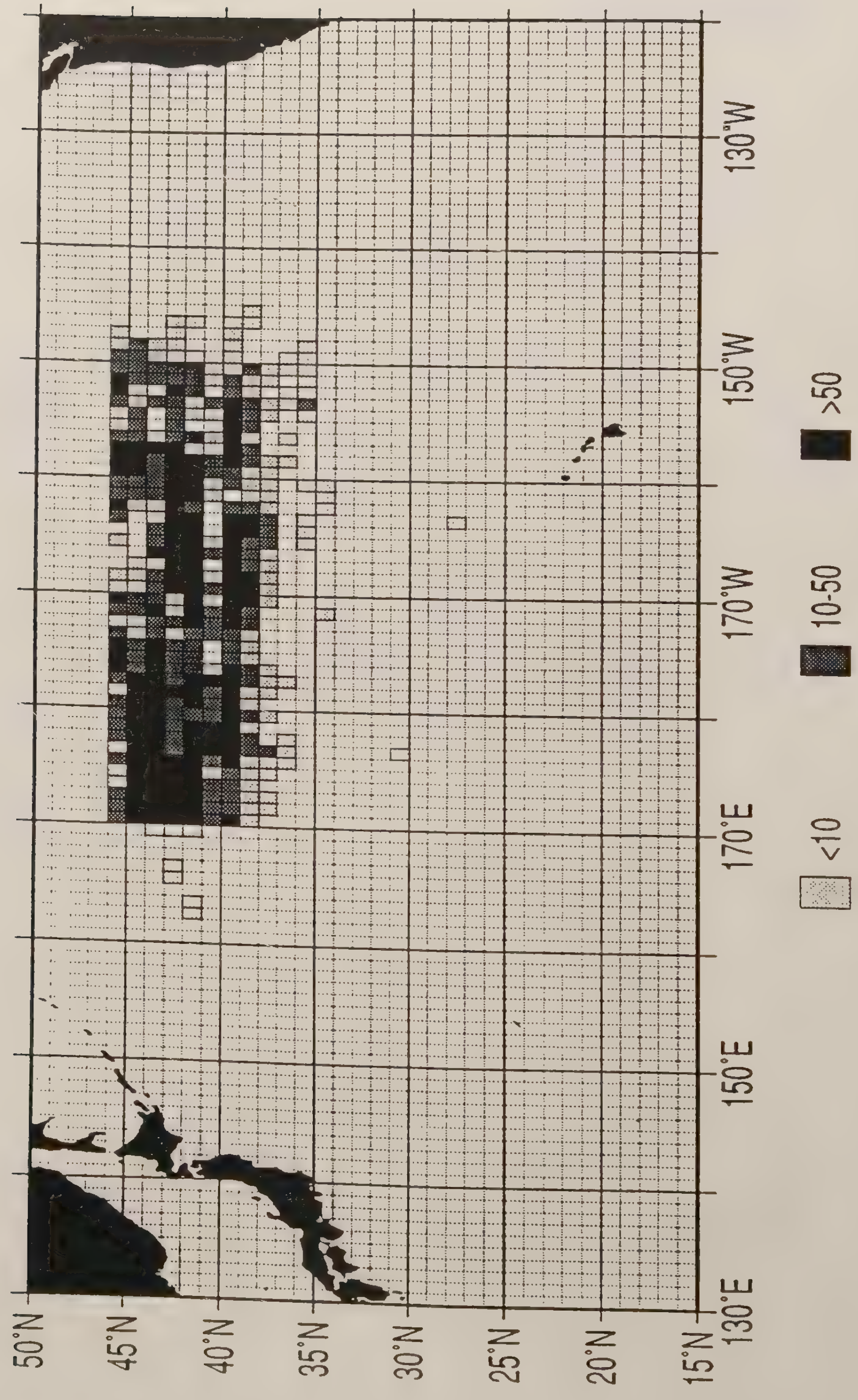
50°N
45°N
40°N
35°N
30°N
25°N
20°N
15°N
130°E
150°E
170°E
170°W
150°W
130°W
<10
10-50
>50

Fig. 3. Distribution of fishing effort in the 1990 Japanese North Pacific high-seas squid driftnet fishery. Units are thousands of standardized (50-m) tans deployed.

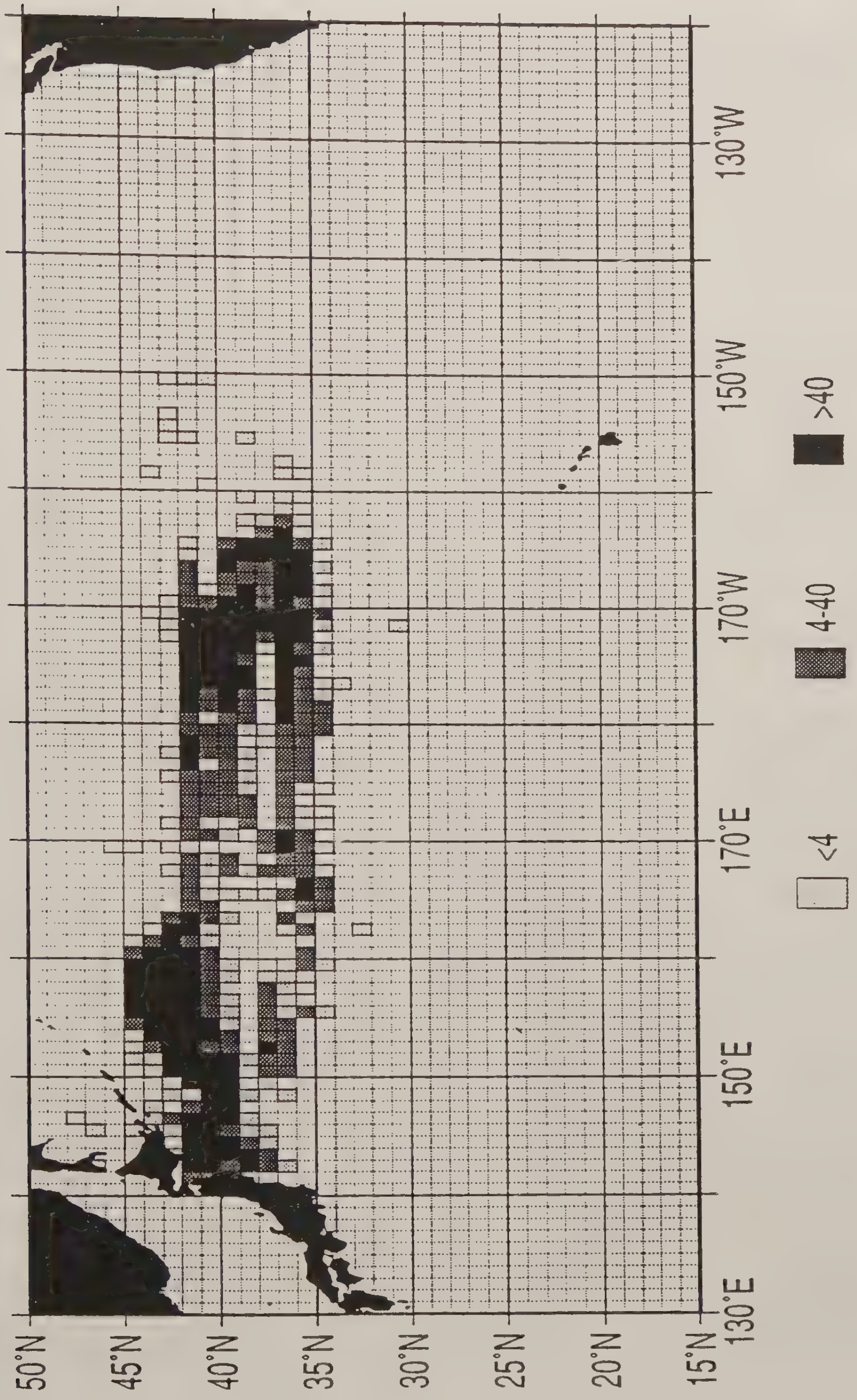
50°N
45°N
40°N
35°N
30°N
25°N
20°N
15°N
130°E
150°E
170°E
170°W
150°W
130°W
<4
4-40
>40

Fig. 4. Distribution of fishing effort in the 1990 Korean North Pacific high-seas squid driftnet fishery. Units are thousands of standardized (50-m) poks deployed.

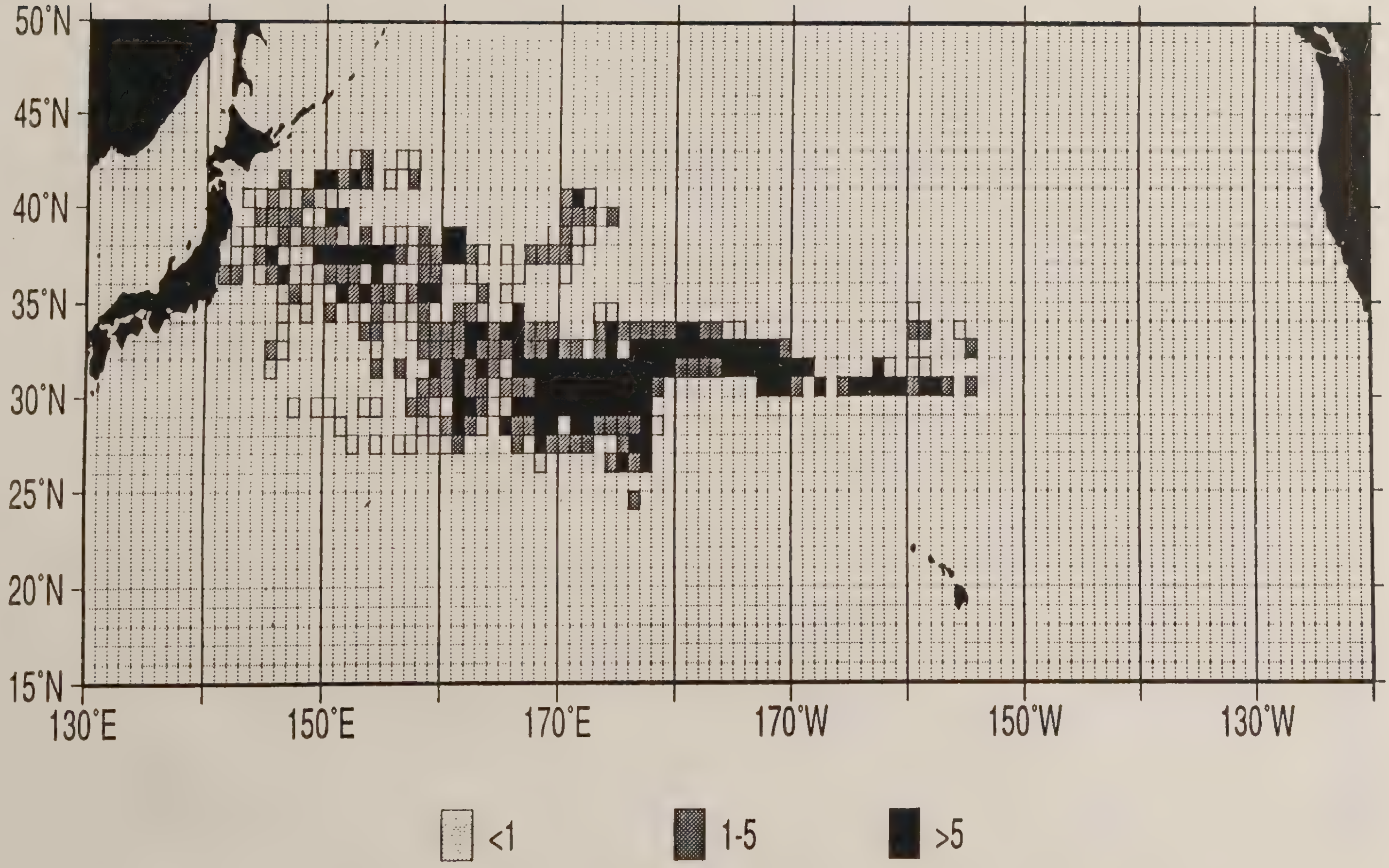
50°N
45°N
40°N
35°N
30°N
25°N
20°N
15°N
130°E
150°E
170°E
170°W
150°W
130°W
<1
1-5
>5

Fig. 5. Distribution of fishing effort in the 1990-1991 Japanese North Pacific high-seas large-mesh driftnet fishery. Units are thousands of standardized (50-m) tans deployed.

Table 2. Estimated bycatch of marine turtles (number of turtles) in the 1990 squid driftnet fisheries of Japan, Korea, and Taiwan, the 1990 large-mesh driftnet fishery of Taiwan, and the 1990-1991 large-mesh driftnet fishery of Japan.

| | Squid Fisheries | | | | Large-Mesh Fisheries | | |
|---|---|---|---|---|---|---|---|
| Species | Japan | Korea | Taiwan | Total | Japan | Taiwan | Total |
| Leatherback | 300 | - | - | - | 45 | 411 | 456 |
| Loggerhead | 5 | - | - | - | 1,200 | 3,489 | 4,689 |
| Green | - | - | - | - | 248 | - | 248 |
| Hawksbill | - | - | - | - | 8 | - | 8 |
| Unspecified hard-shelled | - | - | - | - | - | - | - |
| Unidentified | 101 | - | - | - | - | - | - |
| Total | 406 | 221 | 28 | 655 | 1,501 | 3,900 | 5,401 |

In the 1990 Japanese squid driftnet fishery, observers documented the bycatch of 35 turtles in 2.3 million monitored tans. A simple estimate of total bycatch, given the total fleet effort of 22.8 million tans, is 347 marine turtles. Empirical bootstrap distributions of total bycatch, based on a time-area stratification of the squid driftnet fishery data (Wetherall and Yong 1993), are 375 turtles of all species (approximate 95% confidence limits, 255 and 499), and 264 leatherbacks (approximate 95% confidence limits, 176 and 357). Yatsu and Hayase (1991), using a similar procedure, estimated a total fleet bycatch of 300 leatherbacks, 5 loggerheads, and 101 other (including unidentified) marine turtles.

In the 1990 Korean squid driftnet fishery, the total fleet effort during the April-December fishing season was 24.6 million poks. U.S. and Korean observers monitored 2.7% of the effort, documenting a bycatch of 6 turtles, a bycatch rate of 9.0 turtles per million poks. A simple, direct estimate of the total turtle bycatch by the 1990 Korean squid fleet is therefore 221 turtles. The sample size is too small to allow a reliable division of the bycatch by species.

Estimation of the total turtle bycatch in the 1990 Taiwanese squid driftnet fishery is complicated by the lack of reliable information on total effort by the Taiwanese squid fleet. The official Taiwan government statistics indicate a total effort of 11,266 vessel days of fishing by the combined squid and largemesh driftnet fleets. We assumed that about 1/3 of this effort was directed at squid, or 3,755 vessel days, equivalent to 3,755 fishing operations. U.S. and Taiwanese observers counted 2 turtles in the monitored net sections of 353 fishing operations. The total number of turtles entangled per fishing operation is therefore estimated to be 0.0076, assuming that the observers monitored 75% of the total tans retrieved during the monitored operations. Thus the total marine turtle bycatch for the Taiwanese squid driftnet fleet in 1990 is estimated as 28 turtles. This cannot be reliably partitioned by species.

The combined estimate of 1990 marine turtle bycatch by the three squid driftnet fleets is 655 turtles (Table 2). Because of the very small samples seen in the Korean and Taiwanese fisheries we are reluctant to estimate total bycatches by species.

## 5. Total Bycatch in the Large-mesh Driftnet Fisheries

Fleet effort data for the 1990-1991 Japanese large-mesh driftnet fishery (the season extended from August 1990 through May 1991) were made available just prior to the revision of this paper and we have not yet carefully analyzed them. They indicate, however, a total effort of 2,665,474 standardized tans in 3,488 fishing operations. In 513,367 tans monitored by observers (involving 829 fishing operations), the aggregate bycatch of marine turtles was 289 turtles, or 563.0 turtles per million standardized tans. Expanding this bycatch rate by the total fleet effort provides a provisional total bycatch estimate of 1,501 turtles for the 1990-1991 fishing season. Apportioning the total bycatch according to the observed species composition provides the following bycatch breakdown: 42 leatherbacks; 753 loggerheads; 156 green turtles; 5 hawksbills; and 545 unidentified turtles, of which at least 467 were unspecified hardshelled turtles. A further allocation of the unidentified bycatch according to the species composition of the identified turtles yields the following overall results: 45 leatherbacks; 1,200 loggerheads; 248 green turtles; and 8 hawksbills. These estimates are only rough approximations, and are subject to revision after a more thorough analysis of time-area variations. With respect to precision of the estimates, however, we note that observers monitored 19.2% of the total standardized tans deployed by the fleet, and 23.8% of the fleet's fishing operations.

Estimation of bycatch in the 1990 Taiwanese large-mesh driftnet fishery is complicated by the lack of reliable fishing effort data. There apparently is no way to separate driftnet fleet effort statistics into squid and large-mesh components. The official Taiwan fishing statistics indicate a total driftnet fleet effort of 11,266 fishing operations in 1990. The proportion of these involving large-mesh gear was probably about 2/3, based on the distribution of catch rates of the target species in each fishery, flying squid (*Ommastrephes bartrami*) and albacore (*Thunnus alalunga*). This division suggests a total large-mesh effort of about 7,500 operations. Assuming that observers counted the bycatch in an average of 75% of the total driftnet deployed in each monitored operation, the bycatch rate of marine turtles was about 0.39/0.75 or 0.52 turtles per large-mesh fishing operation. Expanded to the entire fleet, these figures give a rough estimate of 3,900 turtles taken overall by the Taiwanese fleet in 1990. The breakdown by species would be approximately as follows: 411 leatherback turtles; 411 loggerhead turtles; and 3,078 unidentified turtles. Allocating the unidentified turtles is more difficult, but it is likely that most of these turtles were loggerheads. Under this assumption, the composition of the 1990 Taiwanese large-mesh fleet turtle bycatch is estimated to be 411 leatherbacks and 3,489 loggerheads.

Combining these estimates, we judge that the total take of marine turtles in the 1990-1991 season Japanese large-mesh fishery and the 1990 Taiwanese large-mesh fishery was about 5,401 turtles (Table 2). The aggregate species composition was approximately as follows: 456 leatherbacks, 4,689 loggerheads, 248 green turtles, and 8 hawksbills.

The total marine turtle bycatch in the 1990 squid driftnet fisheries of Japan, Korea, and Taiwan, the 1990 large-mesh fishery of Taiwan, and the 1990-1991 large-mesh fishery of Japan was estimated to be 6,056 (Table 2).

## VII. TOTAL MORTALITY IN THE DRIFTNET FISHERIES

### 1. Status, Condition, and Disposition of Turtles in the Bycatch

Driftnet observer data include assessments of the status, condition, and disposition of entangled turtles. All observers noted the condition of turtles encountered, according to the following criteria:

| | | |
|---|---|---|
| *dead* | - | turtle showed no signs of life when it was decked or seen dropping out of the net. |
| *alive* | - | turtle was released alive after being decked, or dropped out of the net alive before being decked, and was thought to have a high probability of survival. |
| *unknown* | - | condition of turtle could not be determined, or turtle was alive but in such poor condition that its survival was considered unlikely. |

In addition to collecting basic data on condition, U.S. observers were required to complete a special data form for each turtle encountered which provided further information on whether the turtle was decked, cut out of the net, or dropped out of the net before being decked.

In the Taiwanese and Korean squid driftnet fisheries, the number of turtles recorded in monitored net sections were too few to assess reliably the proportion of turtles in each condition category. But data from the 1989 and 1990 Japanese squid driftnet fisheries indicate that about 80% of the turtles in the monitored bycatch were released or dropped out "alive".

In the case of large-mesh driftnet fisheries, where more turtles were entangled, better estimates of turtle condition are available. In the 1990-1991 Japanese large-mesh fishery the percentages of turtles in the three categories were:

| SPECIES | TOTAL TURTLES | PERCENT DEAD | PERCENT ALIVE | PERCENT UNKNOWN |
|---|---|---|---|---|
| Leatherback | 8 | 0 | 75 | 25 |
| Loggerhead | 145 | 22 | 73 | 5 |
| Green | 30 | 30 | 63 | 7 |
| Hawksbill | 1 | 100 | 0 | 0 |
| Unspecified Hard-shelled | 90 | 23 | 66 | 11 |
| Unidentified | 15 | 7 | 66 | 27 |
| Total | 289 | 22 | 69 | 9 |

Overall, in the 1990-1991 Japanese large-mesh fishery 22% of the turtles seen entangled in monitored net sections were "dead". In the 1990 Taiwanese large-mesh fishery 32% of the turtles were classified as "dead". Most turtles observed on Taiwanese large-mesh vessels were not identified to species.

Leatherback turtles, which predominated in the monitored squid driftnet bycatch, were typically so large that they dropped out or tore out of the net during retrieval or were cut out of the net without being hauled aboard. Some turtles, particularly leatherbacks, classified as in an "unknown" condition were released alive but swam away from the vessel still entangled in pieces of corkline and webbing. Although the fate of such turtles is unknown, it is highly likely that they eventually died or were debilitated due to continuing entanglement. In the large-mesh fisheries, where a greater number of turtles were encountered, data collected by U.S. observers indicate that 40% of entangled leatherback turtles were decked, compared with 83% of the loggerheads and 100% of the green turtles. U.S. observers noted that decked turtles were often treated harshly by the crews before being returned to the sea.

## 2. Estimates of Total Mortality

Estimates of the *minimum* mortality due to driftnets may be computed by multiplying the total bycatch estimates by the proportions of entangled turtles classified as "dead" at the time of retrieval. This procedure gives only lower bounds to mortality for at least two reasons: (1) the numbers of "dead" turtles probably underestimate the true mortality of turtles entangled in monitored fishing operations, and (2) the mortality rates in monitored operations may underestimate mortality rates in the fleet at large. In regard to the first reason, in each of the other condition categories, "alive" and "unknown", there were undoubtedly some turtles that died later as a result of handling or their entanglement in the driftnet. It is impossible to know how many of such turtles died. However, many turtles in the "unknown" category probably had little chance of survival, since they were still entangled in fragments of driftnet webbing and line or were severely injured. Other turtles in the "alive" or "unknown" categories likely suffered physiological stress or debilitation (Kemmerer 1989, and other studies cited in Eckert 1991) as a result of entanglement or handling. With respect to the second reason, it is at best debatable whether entangled turtles were treated as carefully on driftnet vessels not carrying scientific observers (the vast majority of the fleet) as on vessels with observers, and whether all decked turtles were returned to the sea.

Observer data indicate that in 1990 the Japanese squid driftnet fishery inflicted a minimum total mortality of 81 turtles. Most of the mortality involved leatherbacks. Applying the same criteria and mortality rates to the Korean and Taiwanese squid fisheries, we roughly estimate an aggregate mortality of 131 turtles in the three squid driftnet fisheries in 1990, all species combined.

In the large-mesh fisheries, where more data are available, the following mortality estimates were derived for Taiwan (1990) and Japan (1990-1991 season).

| SPECIES | JAPAN | TAIWAN | COMBINED |
|---|---|---|---|
| Leatherback | 0 | 103 | 103 |
| Loggerhead | 264 | 1,116 | 1,380 |
| Green | 74 | 0 | 74 |
| Hawksbill | 8 | 0 | 8 |
| Total | 346 | 1,219 | 1,565 |

These rough mortality estimates for single fishing seasons provide only a narrow glimpse of the driftnet fishery impacts on marine turtles. A full assessment of impacts would consider the turtle mortality generated by the driftnet fleets over their entire history and geographical range. Unfortunately, sufficient data are lacking. No bycatch data are available prior to the 1989 pilot observer program on Japanese squid vessels, yet the squid driftnet fisheries have been operating since 1979 or 1980. Similarly, the large-mesh driftnet fishery of Japan has been in existence since the early part of this century, with significant offshore expansion occurring in the 1980s. The Taiwanese entry into large-mesh fishing, directed at albacore, has been more recent.

Knowledge of effort history in the large-mesh fisheries is particularly important because of the higher rates of marine turtle bycatch in these fisheries. Only limited data are available, however, on the large-mesh effort prior to 1990. In the case of Taiwan, the combined squid and large-mesh fishing effort in 1989 was 17,598 fishing days, 56% higher than the effort in 1990; the breakdown by fishery is unknown. Likewise, the fishing effort by the Japanese large-mesh fishery was probably greater prior to the 1990-1991 season, when the first observers were deployed, but reliable effort estimates are not available. Fleet data reported by Watanabe (1991) suggest that Japanese large-mesh vessels engaged in roughly 8,300 fishing operations in 1988, considering only those driftnet vessels over 100 gross tons, or 10,300 operations if all vessels over 50 gross tons are included. This is 2.5-3.0 times greater than the total effort reported for the 1990-1991 large-mesh driftnet fishing season. The only data available that might indicate the history of Japanese large-mesh effort is the number of vessels registered to operate in the fishery. In 1988 the number of registered vessels was 459, well below the peak fleet size of 717 vessels in 1982, and below the 1980-1988 mean of 529 registered vessels. These data imply that the average annual effort during 1980-1988 may have been about 9,500-11,900 operations. If turtle bycatch rates in the Japanese large-mesh driftnet fishery throughout the 1980s were similar to the 1990-1991 bycatch rates, that fleet may have killed each year roughly between 1,000 turtles (minimum mortality, as defined above), and 5,000 turtles (if all turtles entangled were killed). Clearly such estimates are highly speculative, but they indicate the possible magnitude of turtle mortality given the best information available.

The minimum total turtle mortality in the North Pacific high-seas driftnet fisheries may have been on the order of 2,500 turtles per year during the late 1980s. The actual mortality was probably greater than this, but less than the estimated total driftnet bycatch of perhaps 9,000 turtles per year. Based on 1990 observer data, most of the mortalities would have been loggerheads taken in the Japanese and Taiwanese large-mesh fisheries.

## VIII. POPULATION IMPACTS

Assessment of the impacts of driftnet fishing on marine turtle populations requires a comprehensive understanding of their biology, population size, population structure, and factors affecting population dynamics. As indicated, to make reliable assessments it is also essential to know the history of mortality in the population, including mortality inflicted by driftnet fisheries. There are large gaps in our understanding, however. Most turtle research has focused on the biology of nesting populations and hatchling production. Little is known about the long juvenile and subadult phases of development, in which the turtles are generally inaccessible. As a result, information on population age structure and survivorship is lacking.

Until much more is known about population structure and abundance, realistic mathematical models of turtle stock dynamics are unfeasible. However, numerical models of population dynamics based on preliminary data may be useful in pointing out critical assumptions, identifying data needs, and suggesting the possible magnitude of impacts.

A significant difficulty in modelling the response of a turtle population to driftnet fishing mortality is uncertainty about the population's resilience to increased mortality. It is reasonable to assume that a turtle population in relatively pristine state has some capacity for compensation, e.g., through increases in density-dependent growth rates or acceleration of reproductive schedules (Wilbur and Morin 1987; Frazer 1983). Faster growth at lower stock densities may shorten exposure to mortality risks and accelerate maturation. We are unaware of evidence of density-dependent growth in marine turtles, but the possibility is suggested by the wide variations in growth rates observed in many populations (Balazs 1982b; Crouse and Crowder 1987). As indicated above, however, any suggestion of density-dependent compensation is speculative. Growth rate variation may be due to factors independent of population density and food supply, such as heredity and ambient temperature. Further, populations already reduced well below pristine levels through harvesting of various life stages, environmental degradation, and other sources of increased mortality may have little remaining capacity for compensation.

### 1. Hawksbill Impacts

The estimated 1990 bycatch of hawksbills in the driftnet fisheries was 8 turtles, based on a single hawksbill identified in the monitored bycatch of the Japanese large-mesh fleet. No hawksbills have been identified in the squid fishery bycatches. This estimate suggests that the impacts of the driftnet fisheries on hawksbill populations are probably minor, barring serious biases in the monitoring programs, much larger bycatches of hawksbills prior to 1990, or the possibility that the turtles killed were offspring of a single, small, isolated nesting colony. In this regard, we note that in the endangered Hawaiian hawksbill population only about 15 females are thought to nest each year. Hawksbill nesting colonies throughout the central and western Pacific are typically small, and most have undergone severe declines from human harvesting for local consumption or international commercial trade.

### 2. Loggerhead Impacts

Some perspective on driftnet mortality impacts may be provided by computing the expected hatchling production and abundance of juveniles and subadult turtles under specific assumptions about stock origin and survivorship. In the case of loggerheads, it is reasonable to assume that most loggerheads taken in the driftnet fisheries originate from nesting colonies in Japan. While a comprehensive inventory of nesting is not available, some data on nesting activity have been reported. For example, Kajihara *et al.* (1991) reported that the number of loggerheads which "landed" on beaches in Kagoshima Prefecture in 1990 was 4,401. This statistic was 2,933 in 1989, 2,725 in 1988, and 2,296 in 1987. We assume that these figures do not refer to the total number of individual females nesting on these beaches, but rather to the aggregate number of emergences or crawls by a smaller number of females hauling out repeatedly during the nesting season. If so, then perhaps 500-1,000 loggerheads nested in Kagoshima Prefecture each year in recent years, assuming 3-6 emergences per nester. Loggerheads also nest in other regions of Japan, and we consider it likely that 2,000-3,000 loggerheads nest annually in Japan. Loggerheads are also known to nest in China and elsewhere in the western North Pacific outside Japan but we do not know the magnitude of these populations.

Nelson (1988) summarized the life history and environmental requirements of loggerheads and reviewed available information on mortality and reproductive biology. Based on his account, we would expect an annual nesting population of 2,000-3,000 loggerheads to produce approximately 600,000-900,000 hatchlings (300 per nesting female) each year. Roughly 0.3-0.4 percent of each brood, according to Nelson (1988), would have to survive to adulthood to maintain the stock at a constant level. Assuming such conditions, one can calculate steady-state, age-specific abundance and natural mortality levels that would prevail under various maturation schedules and survivorship curves. For example, Table 3 shows the expected relative size of the juvenile and subadult population ($X_{js}$), compared with an initial cohort of 600,000 hatchlings, under several combinations of first-year survival rate and age at maturity, assuming a 0.3 percent overall survival from hatchling to adult. The steady-state annual natural mortality levels of juveniles and subadults ($M_{js}$) are also given. The equilibrium abundance and mortality levels for juveniles and subadults are inversely related to first-year survival rate, as expected. Similarly, the steady-state abundance of juveniles and subadults is directly related to age at maturity, and the sustainable mortality rate in these age groups, $1\text{-}S_{js}$, is inversely related to age at maturity.

The wide range of outcomes in Table 3, together with our uncertainty about critical population parameters, point out the difficulty of assessing high-seas driftnet impacts. For example, if age at maturity were 25 yrs and survival during the first year were 25%, a geometric mean survival rate of 83% would be required in juvenile and subadult age classes to maintain the population at equilibrium with a 0.3 percent hatchling-adult survival rate. Under these conditions the steady state abundance of juveniles and subadults would be 1.45 times greater than the annual hatchling production. If 600,000-900,000 hatchlings were produced annually, a juvenile and subadult population of about 870,000-1,300,000 loggerheads would result. The annual mortality to juvenile and subadult loggerheads, under these equilibrium conditions, would be on the order of 150,000-225,000 turtles. On the other hand, if hatchling survival were only 10%, then the number of juveniles and subadults in a steady-state

Table 3. Annual survival rate for juvenile and subadult turtles ($S_{js}$), relative juvenile and subadult population size ($X_{js}$), and annual mortality of juvenile and subadult turtles ($M_{js}$), under various combinations of first-year survival rate and age at maturity, given a hypothetical steady-state hatchling production of 600,000 turtles and hatchling-to-adult survival of 0.3 percent.

| Age at Maturity | | | First-year Survival Rate | |
|---|---|---|---|---|
| | | 10% | 25% | 75% |
| 15 yrs | $S_{js}$ → | 78% | 73% | 67% |
| | $X_{js}$ → | 0.44 | 0.91 | 2.26 |
| | $M_{js}$ → | 58,200 | 148,200 | 448,200 |
| 25 yrs | $S_{js}$ → | 86% | 83% | 79% |
| | $X_{js}$ → | 0.70 | 1.45 | 3.56 |
| | $M_{js}$ → | 58,200 | 148,200 | 448,200 |
| 30 yrs | $S_{js}$ → | 89% | 86% | 83% |
| | $X_{js}$ → | 0.88 | 1.77 | 4.39 |
| | $M_{js}$ → | 58,200 | 148,200 | 448,200 |

population would be considerably lower, as would be the annual mortality sustainable by the population.

The actual abundance and age structure of juvenile and subadult loggerheads in the North Pacific are unknown. The only pertinent information available appears to be the anecdotal report by Bartlett (1989) of an aggregation of immature (20-80 cm CL) loggerheads feeding on pelagic red crab (*Pleuroncodes planipes*) off Baja California Sur, Mexico. Bartlett speculated that there were more than 100,000 turtles involved. Based on tag-and-recapture data (Uchida and Teruya 1991; also see Balazs 1989), juvenile loggerheads in the eastern North Pacific are likely to be from Japanese nesting stocks.

Under some of the conditions given in Table 3, an annual mortality by driftnet fisheries of 1,500 loggerheads, or even 5,000 loggerheads, would have a relatively small impact compared with the total mortality in the population, provided driftnets killed turtles from the younger age groups rather than late subadults and the population compensated adequately. Carapace length data collected by driftnet program observers suggest that juvenile loggerheads were most at risk from driftnet fishing in 1990 (no data are available for earlier years of the large-mesh driftnet fishery). Under other conditions, however, the impacts of a 1,500-5,000 loggerhead kill in driftnets would be very significant. Sufficient data are not available to allow a reliable assessment of actual driftnet impacts. No reliable estimates of juvenile and subadult abundance or survival rates are available. Nor are there data to indicate recent trends in the loggerhead population or the capacity of the population to compensate for fishing mortality.

In any case, the available data indicate that the impacts of the squid driftnet fisheries on North Pacific loggerheads are probably negligible. The impacts of the large-mesh fisheries are greater, but their magnitude cannot yet be reliably determined.

## 3. Green Turtle Impacts

Parallel reasoning can be applied to green turtles to explore a range of possible driftnet fishery impacts. In the case of green turtles the likely sources of turtles taken in the driftnet fisheries include the nesting colonies in Hawaii (mainly at French Frigate Shoals) and Japan (principally in the Ogasawara Islands), each locale about equidistant from the driftnet fishing area where green turtles have been encountered. In the Hawaiian green turtle population, the number of nesting females at the key nesting beach has fluctuated during a 16-yr period of monitoring. But recently the state-wide population of nesting females has averaged about 300-400 females annually, producing about 150,000 hatchlings. The Ogasawara Islands green turtle nesting population has recently numbered about 200 females per year (Suganuma 1985). The combined annual hatchling production from the Hawaiian and Japanese stocks of green turtles may therefore be about 250,000 hatchlings. As with loggerheads, under certain assumptions the estimated 1990 driftnet kill of about 100 green turtles (perhaps 250 if all entangled turtles died), mostly early juveniles, would represent a relatively small fraction of the total juvenile mortality in the population. Again, under other sets of assumptions the impacts would be a great deal more severe.

As with loggerheads, the availsble observer data indicate that impacts of the high-seas squid driftnet fisheries on green turtles are probably negligible. Impacts of the large-mesh fisheries are greater, but cannot be reliably assessed without more information about population trends and natural mortality levels. Nevertheless, stocks of green turtles in Hawaii, Japan, and other locales have been severely reduced over the years. Thus any mortality by the driftnet fisheries will at the very least impede recovery of the populations.

## 4. Leatherback Impacts

The population dynamics of leatherback turtles are even less well understood than those of other marine turtle species. The stock origins of leatherbacks killed in the North Pacific high-seas driftnet fisheries are unknown. The possibilities include nesting colonies in Mexico, where an estimated 30,000 females may nest each year (Pritchard 1982); Irian Jaya, Indonesia, where some 13,000 nests (equivalent to about 2,000 nesters) were recorded in 1985 (Bhaskar 1985); Malaysia and China. The number of nesters in the Chinese population of leatherbacks is unknown. The nesting population in Terengganu, Malaysia, once substantial, has declined severely over the past 35 years, due primarily to heavy egg depredation. The estimate of beach landings by nesting leatherbacks at Terengganu dropped to only 280 in 1985, down from about 11,000 landings in 1956 (various sources cited by Eckert 1991). At any rate, the total Pacific leatherback hatchling production from these various sources is probably several million hatchlings per year.

The impacts of the driftnet mortality clearly depend on the stock origins of the leatherbacks encountered in the fisheries. If the leatherbacks killed in the driftnet fisheries are from the stocks nesting in Mexico or Indonesia, the driftnet fisheries would appear not to be a significant source of mortality to the population(s), compared to other sources. However, if the leatherback mortality in the driftnets involves turtles from the Malaysian stock exclusively the impact would be significant, since the driftnets appear to take mostly subadult or adult leatherbacks. Recovery of the Terengganu leatherback population will require protection of nests and a halt to egg depredation. But such measures would be ineffective without equal efforts to reduce mortality to the sharply declining numbers of adults and subadults (Crouse and Crowder 1987). There are no data to indicate whether the leatherbacks taken in the driftnet fisheries are from the depleted Terengganu population, from the more robust stocks in Mexico or Indonesia, or from a multitude of stocks. The issue cannot be resolved without information on leatherback stock structure and migration routes. Leatherback impacts appear to be of similar magnitude in the squid and large-mesh driftnet fisheries, probably because the species is distributed throughout the fishing grounds.

To summarize, a comprehensive, reliable assessment of the impacts of North Pacific high-seas driftnet fisheries on marine turtles is impossible without a better understanding of turtle population sizes, stock origins, exploitation history, and population dynamics. Under certain assumptions about stock origins, survivorship, and other parameters it may be argued that the mortality inflicted by driftnet fisheries in 1990, when all fisheries were monitored, had relatively little impact on marine turtle populations compared with other sources of mortality. Under other assumptions it may be concluded that driftnet fishing mortality was indeed significant.

Nevertheless, incidental mortalities of marine turtles in high-seas driftnet fisheries add to losses due to other factors, many of which have not abated or have even accelerated. Driftnet mortalities therefore impede national and international efforts to recover marine turtle populations, all of which are classified either as endangered or threatened by the IUCN.

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# A Comparison of Driftnet Fishery Bycatch Estimation Methods Based on Empirical Bootstrap Distributions

by
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## I. ABSTRACT

Two methods were compared for estimating the total bycatch of albacore (*Thunnus alalunga*), skipjack tuna (*Katsuwonus pelamis*), and blue shark (*Prionace glauca*) in the 1990 Japanese driftnet fishery for neon flying squid (*Ommastrephes bartrami*): (1) a standard method that expands the arithmetic mean of sample bycatch rates, and (2) the Pennington method which expands the delta-lognormal estimator of the mean bycatch rate. Bootstrap distributions of the two estimators consistently showed that the Pennington method estimated higher total bycatch and wider approximate confidence intervals for total bycatch. The results agree with other findings published recently, indicating that the Pennington estimator is not robust with respect to the key assumption of lognormality in the positive bycatch rates.

## II. INTRODUCTION

Estimates of bycatch levels in the high-seas driftnet fisheries may vary substantially depending on the statistical method used. Whether the statistical method is applicable and the resulting estimates useful depends on the validity of critical underlying assumptions. Using data from the 1990 Japanese fishery for neon flying squid (*Ommastrephes bartrami*), we compared bycatch estimates from two procedures: (1) a standard method that expands the arithmetic mean of sample bycatch rates, and (2) a method which expands the delta-lognormal estimator of mean bycatch rate. The latter method is derived from ideas first developed by Aitchison (1955) and introduced to fishery surveys by Pennington (1983). Empirical bootstrap distributions of each estimator were computed. In both cases, total bycatch was estimated for specified time-area strata and then summed over the strata.

## III. BYCATCH RATE AND FISHING EFFORT DATA

The data for bycatch estimation consist of observations of bycatch rates for a sample of fishing operations by selected Japanese commercial squid driftnet vessels, and statistics on fishing effort by the total squid driftnet fleet. The fleet effort data were provided by the Japan Fisheries Agency (JFA). The bycatch data were collected by Canadian, Japanese, and U.S. scientific observers deployed on squid driftnet vessels in 1990. Observers were deployed on selected squid driftnet vessels at the discretion of the JFA with a view to achieving representative coverage of the fleet's total effort.

A fishing operation on a Japanese squid driftnet vessel involves the deployment of several independent driftnet sections. A section consists of about 100 net panels or "tans", each 35-50 m long and about 8 m deep, joined together. In a typical operation the setting of the net sections begins around dusk, and retrieval commences before dawn the following day. Although retrieval usually takes 8-12 hours, it may be slower if squid catch rates are extremely high or other difficulties occur. Then, some driftnet sections may be left in the water one or two additional nights. Such extended retrievals occurred in 4.6% of the operations monitored by observers in 1990.

Observers collected bycatch data from a subset of the driftnet sections that were set and retrieved during each monitored fishing operation. Observers usually monitored 6-7 sections out of the 7-10 sections typically deployed. Observers decided which sections to monitor at the beginning of the operation based on tables of random numbers. The sampling tables and all other bycatch observation procedures were developed and standardized jointly by the three countries. For the purposes of this analysis, bycatch data from all monitored sections of a fishing operation were pooled.

Bycatch rate statistics for each species caught in the operation were computed by dividing the pooled bycatch by the pooled fishing effort (standardized as the number of 50-m tan equivalents). The bycatch rate for each species, expressed as the number of animals decked per 1,000 standardized tans of monitored fishing effort, was associated with the exact position and date of the operation. Statistics on the fleet's fishing effort, expressed as the number of standardized tans deployed, were available only in summarized form for each 10-day period and 1° latitude x 1° longitude cell within the regulated squid driftnet fishing area.

## IV. STRATIFICATION

Bycatch rate data and fleet effort statistics were stratified by month (May through December) and longitude (145°W-160°W, 160°W-175°W, and 175°W-170°E). The fleet did not operate in some time-area strata. Further, some strata had low effort and no observer coverage, particularly late in the year. Fleet effort and bycatch rate statistics from such strata were pooled with data from adjacent strata. As a result, there were 19 time-area strata overall (Table 1).

In addition, each time-area stratum was divided into two substrata, one consisting of all 1° latitude x 1° longitude cells in which observer data were available (substratum A) and the other consisting of the remaining cells with no observer coverage (substratum B).

## V. BYCATCH ESTIMATORS

Two bycatch estimators were compared. The first is the standard method employing the arithmetic mean bycatch. In this simple approach bycatch in each time-area stratum is estimated by calculating the arithmetic mean of the bycatch rates over all monitored operations within the stratum, then multiplying the mean bycatch rate by the total fleet effort (see below) in the stratum. Total bycatch is estimated as the sum of the individual stratum bycatch estimates. Under the usual assumptions regarding random sampling within each stratum, the standard estimator is unbiased.

Table 1. Summary of 1990 fishing effort, by month and area, for the entire Japanese squid driftnet fleet and for the subset of driftnet vessels on which observers were deployed.

| Stratum | Month | Area[1] | Total fleet | | Monitored vessels | |
|---|---|---|---|---|---|---|
| | | | Operations | 1,000 tans | Operations | 1,000 tans |
| 1 | May | C | 12 | 14 | 14 | 12 |
| 2 | | E | 67 | 84 | 62 | 59 |
| 3 | | W | 31 | 35 | 36 | 31 |
| 4 | June | C | 2,422 | 2,709 | 357 | 310 |
| 5 | | E | 730 | 832 | 163 | 143 |
| 6 | | W | 1,640 | 1,542 | 237 | 186 |
| 7 | July | C | 4,317 | 4,255 | 704 | 568 |
| 8 | | E | 862 | 868 | 171 | 140 |
| 9 | | W | 2,833 | 2,410 | 214 | 139 |
| 10 | August | C | 434 | 413 | 58 | 44 |
| 11 | | E | 1,204 | 1,186 | 273 | 220 |
| 12 | | W | 3,356 | 2,874 | 310 | 220 |
| 13 | September | C | 393 | 390 | 49 | 39 |
| 14 | | E | 94 | 94 | 18 | 16 |
| 15 | | W | 2,176 | 2,123 | 153 | 115 |
| 16 | October | C | 317 | 317 | 14 | 12 |
| 17 | | W | 1,988 | 1,902 | 111 | 91 |
| 18 | November | W | 683 | 638 | 29 | 23 |
| 19 | December | W | 84 | 74 | 7 | 6 |
| Total | | | 23,643 | 22,759 | 2,980 | 2,374 |

[1] E = 145W-160°W, C = 160W-175°W, W = 175W°-170°E

The second method is known as the Pennington estimator (Pennington 1983). It assumes that the time-space distribution of the species of interest is patchy: The species either does not occur in the bycatch (zero bycatch rate) or does occur at some variable frequency such that the positive bycatch rates follow a lognormal distribution. Accordingly, the distribution of the bycatch rates is described by the delta-lognormal mixture distribution (Aitchison and Brown 1957). The mean bycatch rate is estimated under this assumption, then expanded by total effort as in the standard method.

More explicitly, within a given time-area stratum let n represent the total number of sampled operations, and let m denote the number of operations with positive bycatch. Let $x_i$ be the bycatch rate for the $i^{th}$ operation within the stratum, and for operations with positive bycatch, let $y_i = \log(x_i)$. Let $x_{bar}$ denote the arithmetic mean of all the $x_i$; $y_{bar}$, the arithmetic mean of the $y_i$; and s, the standard deviation among the $y_i$. In the standard estimation method, the mean bycatch in the time-area stratum, u, is estimated by the arithmetic mean bycatch, $u_s = x_{bar}$. In the Pennington method, u is estimated by the statistic $u_p$, where

$$u_p = \begin{cases} (m/n)*\exp(y_{bar})*H(m-1)/2; & \\ \qquad (s/4)*(m-1)/m & m>1 \\ x_1/n & m=1 \\ 0 & m=0 \end{cases}$$

is the minimum variance unbiased estimator of u under the delta-lognormal assumption (Crow and Shimizu 1988). The symbol H{.} denotes the hypergeometric function defined as

$$H\{a;z\} = $$
$$1 + z/f_1(a) + z^2/[2*f_2(a)] + \ldots + z^j/[j!*f_j(a)] + \ldots$$

where

$$f_j(a) = \begin{cases} a*(a+1)*(a+2)*\ldots*(a+j-1) & j\geq 1 \\ 1 & j=0 \end{cases}$$

As in the standard method, overall bycatch is estimated by summing the bycatch estimates for individual strata. If sampling is random and the positive bycatch rates are truly lognormal, the Pennington estimator is unbiased, and more efficient than the standard estimator based on the arithmetic mean bycatch.

In computing bycatch within each time-area stratum, two options were explored to expand the mean bycatch rate. In the first option, the bycatch rate in substratum A was assumed to be applicable to substratum B, so the total bycatch for the time-area stratum was computed by multiplying the mean bycatch rate by the total fleet effort in the two substrata:

*Option 1*: $C = u*(E_A + E_B)$
(effort) $\quad = u*E_A*(1 + (E_B/E_A)) \qquad E_A > 0,$

where C is the total bycatch and $E_A$ and $E_B$ are the respective fleet effort levels.

In the second option, the fleet effort in substratum B was ignored, and information on the fleet's decked catches within the substrata were used to expand the bycatch rate:

*Option 2*: $C = u*E_A*(1 + (W_B/W_A)) \qquad W_A > 0,$
(weight)

where $W_B$ and $W_A$ are the reported decked catches in the A and B substrata. The second option makes no assumptions about the relative bycatch rates in the two substrata, but assumes that discard rates, average weights of decked animals, and reporting rates for the species in question are the same in both substrata.

We demonstrate the two methods by applying them to bycatch data for albacore (*Thunnus alalunga*), skipjack tuna (*Katsuwonus pelamis*), and blue shark (*Prionace glauca*). Overall frequency distributions of bycatch rates for albacore, skipjack tuna, and blue shark were skewed strongly to the right (Figs. 1-3). When aggregated over time-area strata, the distributions of the log-transformed positive bycatch rates were not particularly normal. But they appeared to be nearly normal in many individual strata, suggesting that the Pennington estimator would be appropriate and provide estimates of total bycatch with greater precision than the standard estimator.

## VI. BOOTSTRAP SAMPLING

We compared the performance of the two estimators by generating their "bootstrap distributions" from the following Monte Carlo algorithm:

(1) Within each time-area stratum, the observed bycatch rate distribution was taken to be the non-parametric maximum likelihood estimator of the true bycatch rate frequency distribution. Data from all of the monitored fishing operations within the stratum were included, whether or not they involved extended retrievals.

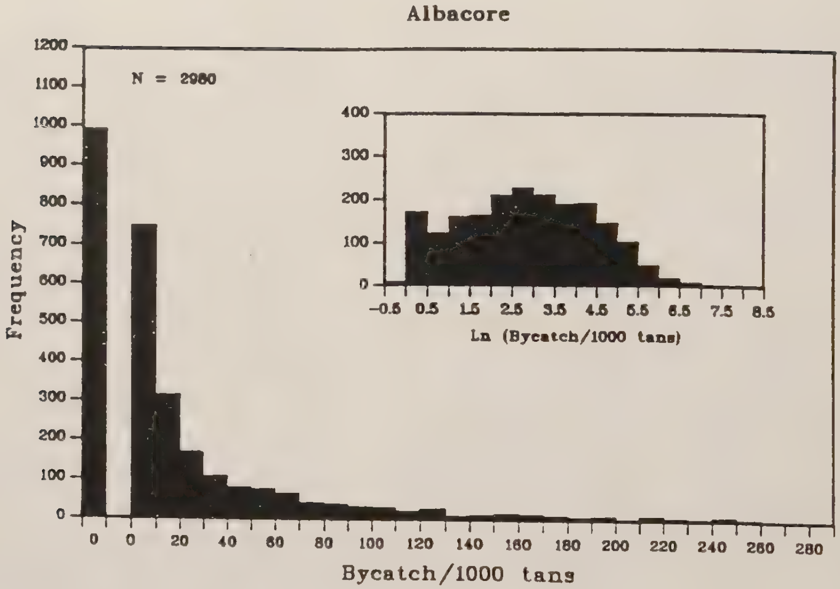

Figure 1. Bycatch rate frequency distribution for albacore in the 1990 Japanese squid driftnet fishery. Inset shows corresponding frequency distribution for log-transformed positive bycatch rates.

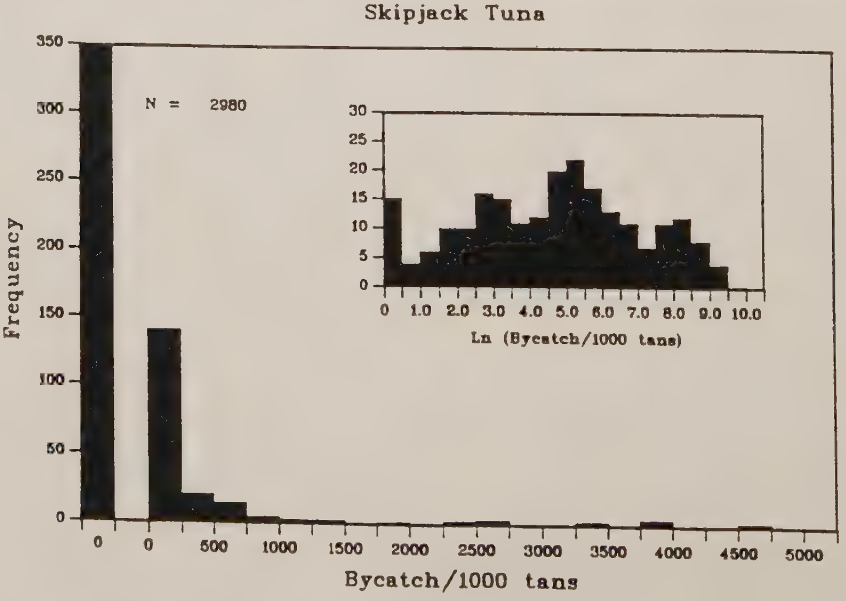

Figure 2. Bycatch rate frequency distribution for skipjack tuna in the 1990 Japanese squid driftnet fishery. Inset shows corresponding frequency distribution for log-transformed positive bycatch rates. For ease in plotting the frequency of operations with zero bycatch rate was truncated at 350; the actual frequency was 2,771 operations.

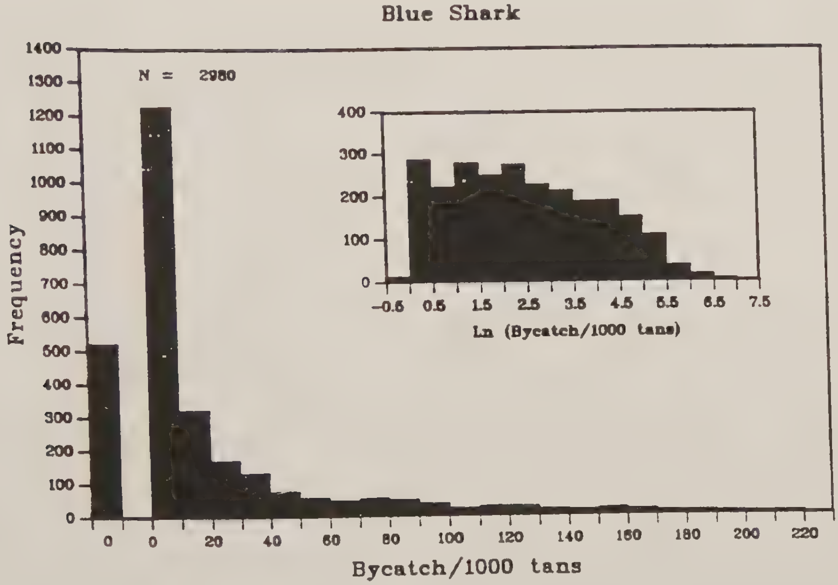

Figure 3. Bycatch rate frequency distribution for blue shark in the 1990 Japanese squid driftnet fishery. Inset shows corresponding frequency distribution for log-transformed positive bycatch rates.

(2) A random "bootstrap" sample was taken (with replacement) from the empirical bycatch rate distribution in each time-area stratum. Sample sizes in each stratum were equal to the number of fishing operations monitored by observers.

(3) The two bycatch estimators were applied to each set of bootstrap sample values, producing a corresponding bootstrap "replicate" pair of total bycatch estimates.

(4) Steps (2) and (3) were repeated 1,000 times (1,000 replicates), generating empirical frequency distributions of total bycatch estimates under the two estimation procedures.

In the Monte Carlo procedure, random bycatch rates were computed by the inverse transformation method (Naylor *et al.* 1966). The required uniformly distributed pseudorandom variates were generated using the *ran1* algorithm described by Press *et al.* (1988).

The bootstrap bycatch distributions are Monte Carlo approximations to the non-parametric maximum likelihood estimators of the true frequency distributions (Efron 1982). As such, they provide an empirical basis for comparing the estimation methods. We evaluated the estimators on the basis of their relative bias and precision. To examine relative bias, we compared the expected values of the estimators, as indicated by their bootstrap distribution means. Specifically, we computed the relative bias of the Pennington estimator as the amount by which its bootstrap distribution mean exceeded the standard estimator bootstrap mean, expressed as a percentage of the latter. Assuming random sampling within strata, this measure is sensitive to violations of the critical assumptions of the Pennington method. To examine estimator precision, we computed the coefficients of variation and the 5th and 95th percentiles of the bootstrap distributions. The percentiles are bootstrap approximations of the upper and lower 90% confidence limits for total bycatch.

## VII. RESULTS

A comparison of the bootstrap distribution means (Table 2) for albacore, skipjack tuna, and blue shark shows that, on average, the Pennington method estimated higher bycatches than did the standard method. The comparisons are based on the Option 1 expansion. The difference was smallest for blue shark (+6.1%), intermediate for albacore (+14.2%), and largest for skipjack tuna (+205%).

Table 2. Characteristics of bootstrap distributions of total bycatch (number of fish) for two bycatch estimators, based on 1,000 replicates. Data are for the 1990 Japanese squid driftnet fishery.

| SPECIES | ESTIMATOR | 5th PERCENTILE $(X10^5)$ | MEAN $(X10^5)$ | 95th PERCENTILE $(X10^5)$ | COEFFICIENT OF VARIATION |
|---|---|---|---|---|---|
| Albacore | Standard | 7.203 | 8.077 | 9.095 | 0.0699 |
| | Pennington | 8.189 | 9.221 | 10.426 | 0.0736 |
| | Relative bias | 13.7% | 14.2% | 14.6% | 5.3% |
| Skipjack tuna | Standard | 21.987 | 29.193 | 36.752 | 0.1536 |
| | Pennington | 50.037 | 88.922 | 148.022 | 0.3708 |
| | Relative bias | 128% | 205% | 303% | 141% |
| Blue shark | Standard | 6.259 | 6.656 | 7.080 | 0.0380 |
| | Pennington | 6.554 | 7.060 | 7.586 | 0.0444 |
| | Relative bias | 4.7% | 6.1% | 7.1% | 16.8% |

These results are consistent with the apparent differences among species in distribution patchiness, at least at the scale measured in a fishing operation. In particular, the differences between the standard and Pennington estimates are directly related to the proportion of zero-bycatch operations in the data.

In estimating total bycatch, the Option 1 expansion gave results differing only slightly from results under the Option 2 approach (Table 3). The similarity between the estimates indicates that observer placement was geographically well-balanced in 1990. (By contrast, observer coverage in the 1989 pilot observer program on Japanese squid vessels was relatively poor in the southern extremity of the fishing area. Consequently, when we estimated the 1989 bycatch of skipjack tuna, which are more abundant in the lower latitudes, Option 2 produced a better estimate than did Option 1.)

As expected, differences between the standard arithmetic mean method and the Pennington method in regard to the 5th and 95th percentiles followed the same pattern as seen in distribution means (Table 2). The differences were smallest in blue shark (+4.7% in the 5th percentile, +7.1% in the 95th percentile), intermediate in albacore (+13.7%, +14.6%), and largest in skipjack tuna (+128%, +303%).

The Pennington estimator is unbiased (and equivalent to the standard arithmetic mean estimator) when the data are truly delta-lognormal. Differences between Pennington estimates and simple arithmetic mean estimates of bycatch would not necessarily be of concern if we were comparing single instances of the statistics calculated from all the bycatch data. The large differences between the bootstrap distribution means, however, indicate a systematic bias in the Pennington estimator. We suspect that the bias is due to failure of the key assumption of the Pennington method. In recent computer simulation experiments, Myers and Pepin (1990) showed that slight departures from lognormality in the positive data values can lead to serious upward bias in the Pennington estimator of the distribution mean.

When the positive bycatch rates are truly lognormal, the Pennington estimator of total bycatch, besides being unbiased, is more precise than the simple arithmetic mean estimator. Indeed, this is the chief motivation for using the Pennington method. But our data show that the coefficients of variation of the bootstrap distributions were consistently higher for the Pennington estimator than for the standard arithmetic mean estimator: albacore, +5.3%; blue shark, +16.8%; skipjack tuna, +141% (Table 2). These results confirm the simulation studies by Myers and Pepin (1990), which showed a steady loss of efficiency, relative to the arithmetic mean estimator, when the lognormal assumption was violated.

Our experience adds to a growing body of results, indicating that the Pennington estimator, despite its theoretical attractions, is not very robust and may often be inappropriate. This seems to be the case for driftnet bycatch estimation. In most instances, non-parametric estimates based on bootstrap distributions of the simple arithmetic mean bycatch rate would be preferable.

Table 3. Bootstrap estimates of total bycatch (number of fish) for two expansion options, based on 1,000 replicates. The standard arithmetic mean estimator was used. Data are for the 1990 Japanese squid driftnet fishery.

| SPECIES | EXPANSION OPTION | BYCATCH ESTIMATE ($x10^3$) | COEFFICIENT OF VARIATION |
|---|---|---|---|
| Albacore | 1 - effort | 8.077 | 0.0699 |
| | 2 - weight | 8.019 | 0.0697 |
| Skipjack tuna | 1 - effort | 29.193 | 0.1536 |
| | 2 - weight | 30.724 | 0.1510 |
| Blue shark | 1 - effort | 6.656 | 0.0380 |
| | 2 - weight | 6.551 | 0.0360 |

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# NOTES

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## Sex Ratio of Immature Green Turtles Inhabiting the Hawaiian Archipelago

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A variety of reptiles possess temperature-dependent sex determination (TSD) (see reviews by Bull, 1980; Raynaud and Pieau, 1985; Ewert and Nelson, 1991; Janzen and Paukstis, 1991), including all species of sea turtles examined to date (Yntema and Mrosovsky, 1980; Morreale et al., 1982; McCoy et al., 1983; Mrosovsky et al., 1984; Dalrymple et al., 1985; Rimblot et al., 1985). Sea turtle sex ratios resulting from TSD are of ecological and conservational significance, since they affect reproduction. Further, a comprehensive knowledge of naturally-occurring sex ratios is a prerequisite for understanding the evolutionary basis of the wide range of sex ratios reported for reptiles with TSD (Bull and Charnov, 1988, 1989). In the current study, a serum androgen sexing technique is used to estimate the sex ratio of immature green turtles, *Chelonia mydas*, inhabiting certain foraging grounds of the Hawaiian Archipelago.

Turtles were captured at Punalúu Bay (19°N, 155°W) and Kiholo Bay (20°N, 156°W) off the island of Hawaii with large mesh tangle nets made of 2.0 mm nylon line. Nets were set at night vertically through the water column at shallow (<3.0 m) foraging grounds frequented by turtles (Balazs et al., 1987). The nets were checked every 30 min or less to remove entangled turtles. Turtles were also captured at nearshore foraging grounds off Palaau (21°N, 157°W) on the island of Molokai. At this location, a pound net was used during the night, and turtles were removed from its central enclosure just after sunrise. Turtles were captured during a time period spanning from 17 December 1983 to 30 August 1984. At all three locations, turtles were taken to shore after capture, and then measurements and blood samples were taken prior to the turtles being released into the wild. Blood samples were taken from the bilateral cervical sinus as described by Owens and Ruiz (1980). Following centrifugation, sera were decanted, temporarily placed on ice, and then transferred into a ≤20 C freezer until they were assayed.

A serum androgen sexing technique was used to sex the immature sea turtles (Owens et al., 1978; Wibbels et al., 1987, 1991; Wibbels, 1988). A detailed description of the testosterone radioimmunoassay procedure, including validation with sera from immature *C. mydas*, has been reported previously (Wibbels et al., 1987, 1990, 1991; Wibbels, 1988). A total of three assays were conducted during this study. Extracted water blanks were included in duplicate in all assays, and they consistently generated values under the sensitivity of the assay. A minimum of two control samples also were included in each assay. The intraassay coefficient of variation was 8.2%, and the interassay coefficient of variation was 23.9%. Assay sensitivity averaged 3.12 pg, and extraction efficiency averaged 73.0%. The testosterone levels of three of the turtles fell within an overlap zone between male and female ranges (Wibbels et al., 1987; Wibbels, 1988). Therefore, those three turtles were not used in estimating the sex ratio.

Sixty-six turtles were captured during this study

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TABLE 1. Sex ratios of immature green turtles captured on Hawaiian foraging grounds.

| Location | Female | Male | Unknown[a] | N | Size range[b] | Sex ratio[c] |
|---|---|---|---|---|---|---|
| Punaluu | 19 | 16 | 0 | 35 | 39.8 to 75.3 | 1.19:1.00 |
| Kiholo | 2 | 2 | 0 | 4 | 48.2 to 66.3 | 1.00:1.00 |
| Palaau | 11 | 13 | 3 | 27 | 39.6 to 71.8 | 0.85:1.00 |
| Pooled | 32 | 31 | 3 | 66 | 39.6 to 75.3 | 0.96:1.00 |

[a] Turtles with serum androgen concentrations greater than 20 pg/ml and less than 30 pg/ml (see text).

[b] Straight carapace length in cm.

[c] Male : female.

(Table 1). Their straight-line carapace lengths (SCLs) ranged from 39.6 to 75.3 cm ($\bar{x} = 58.5 \pm 1.2$ SE), indicating that all turtles were immature since minimum SCL recorded for adult turtles in this population is approximately 80.0 cm (Balazs, 1980; Balazs et al., 1987). Straight carapace lengths did not differ significantly between capture locations (ANOVA, $P > 0.05$). Additionally, the predicted sex ratios from the three capture locations were not significantly different from one another (replicated goodness of fit test, $P > 0.05$). The pooled sex ratio (0.96 females : 1.00 males; see Table 1) did not differ significantly from a 1:1 sex ratio (replicated goodness of fit test, $P > 0.05$). To investigate possible variation in sex ratios relative to size class of turtle, the data were divided into subsets based on SCL. In the first instance, the sex ratio of turtles with SCLs greater than the mean SCLs of the entire group (57.5 cm) was compared to that of turtles with SCLs less than the mean SCL. In the second instance, the mean SCL of each subset was used to generate two additional subsets, and the sex ratios of the four groups were compared. In both cases no significant differences between sex ratios were detected (replicated goodness of fit tests, $P > 0.05$).

Green turtles are the most abundant sea turtle species in Hawaiian waters, and they are members of a single population which appears genetically isolated from other central Pacific populations (Balazs, 1980, 1982a). Turtles in the population appear to mature slowly, requiring an average of approximately 26 yr to reach sexual maturity (Balazs, 1982b). The wide range in the size of turtles captured in the current study suggests that this sampling included turtles produced from numerous year classes of hatchlings. Thus, the sex ratio represents a distillation of many hatchling sex ratios. The data from the current study suggest a sex ratio approximating 1:1, which appears homogenous relative to capture location and size of turtle. If this sex ratio of immature turtles reflects the primary sex ratio in this population, then the data are consistent with the 1:1 ratio predicted by sex allocation models initially predicted by Fisher (1930). However, although hatchling and adult sex ratio appear to correspond in some turtle species (Ewert and Nelson, 1991), the relationship between the sex ratios in the hatchling, immature, and adult portions of a sea turtle population is not clear (Mrosovsky et al., 1984; Wibbels et al., 1987, 1991). Thus, one must be cautious when interpreting the evolutionary significance of results such as those in the current study.

Regardless of the evolutionary implications, the results of the current study are consistent with those of a previous study of immature sea turtles (Limpus and Reed, 1985) suggesting that temperature-dependent sex determination is capable of producing unbiased sex ratios in sea turtle populations. However, studies of other sea turtle populations suggest that female-biased sex ratios (Wibbels et al., 1987, 1991; Mrosovsky and Provancha, 1989, 1991) and male-biased sex ratios (Limpus, 1985; Mrosovsky et al., 1992) may also exist. Wide variation in sex ratios has also been reported in freshwater and terrestrial turtles with TSD (reviewed in Ewert and Nelson, 1991). While several hypotheses have been proposed to account for this variation and for the existence of skewed sex ratios (reviewed in Ewert and Nelson, 1991), their validity is currently unknown. The gradual accumulation of population sex ratio data should provide some insight as to the basis of this variation. However, a thorough understanding of this subject will require comprehensive studies which (1) examine population sex ratios relative to factors affecting sex ratio such as the physical parameters of nesting beaches, reproductive ecology, and nesting behavior in a given population, and (2) compare sex ratios of different age classes of turtles (e.g., hatchlings, juveniles, subadults, adults) within a population.

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# Population biology of *Gnathophausia longispina* (Mysidacea: Lophogastrida) from a central North Pacific seamount

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**Abstract.** Large numbers of the lophogastrid mysid *Gnathophausia longispina* were discovered in 1984 over Southeast Hancock Seamount on the northern Hawaiian Ridge. Additional specimens were collected from the same area during subsequent surveys in 1985, 1987, and 1988 to obtain new information on the life history of this species. Estimates of growth suggest that *G. longispina* reaches sexual maturity by its second year. Young are brooded by the female for nearly a year and released in late winter–early spring. It is doubtful if *G. longispina* live longer than 2 yr or produce more than one brood. Most *G. longispina* are found within 100 m above the seamount summit. The modal progression of size classes over time indicates that this species is dependent on local processes rather than recruitment from other areas to maintain its populations at the seamount.

## Introduction

Many mysid species are characterized by swarming or schooling behaviors which may make them locally very abundant (Mauchline 1980, 1986, Wittmann 1984). Such aggregated distributions have frequently been seen in continental shelf and slope regions and are often attributed to behaviors involved in reproduction, feeding, predator avoidance, or population maintenance within a restricted zone of occurrence (Clutter 1967, 1969, O'Brien 1988, Kaardvedt 1989). Unusual aggregations of some sound scatterers were noted during accoustic observations over a seamount on the northern Hawaiian Ridge in 1984 by the National Marine Fisheries Service, Honolulu Laboratory. Midwater trawls revealed the dominant species in the scattering layer to be the lophogastrid mysid *Gnathophausia longispina* and the sternoptychid fish *Maurolicus muelleri* (Boehlert 1988). Despite these collections, little is known about the biology and distribution of *G. longispina*. The genus *Gnathophausia* belongs to the suborder Lophogastrida and includes eight species (Mauchline 1980). Four species in the genus are cosmopolitan, one is found only in the Atlantic Ocean, and the others are restricted to the Pacific or Pacific and Indian Oceans. *G. longispina* is considered to have the most restricted geographical distribution in the Pacific, and has only been taken west of 157°W in the tropical and north temperate regions between 7°36′S and 31°40′N (Clarke 1962). It is probably the shallowest-dwelling species in the genus (Clarke 1962).

What little reported information exists on the life history of *Gnathophausia longispina* is based on a total of fewer than 200 specimens collected from several surveys between the late 1800's and mid-1900's (Clarke 1962, Mauchline 1980). Consequently, information on vertical distribution patterns, size at maturity, and other biological traits of *G. longispina* is nonexistent or based on only one or a few specimens (Clarke 1962). The present study provides biological information on *G. longispina* based on a large number of specimens taken over several years from a single seamount in the subtropical North Pacific.

## Materials and methods

The study site was Southeast Hancock Seamount (29°48′N; 179°04′E) near the northern edge of the North Pacific central water mass and accompanying subtropical frontal zone (Roden 1984). The flat-topped summit of this seamount is about 2.4 km in diameter (4.5 km$^2$) at a depth of ~260 m; it is the highest of several peaks collectively called Hancock Seamount (Brainard 1986). Bottom depths reach 5200 m approximately 22 km from the summit to produce an average slope along the flanks of 0.22 (Brainard 1986). Water temperatures generally are about 19 to 27°C at the surface, 13 to 15°C at the summit depth, and 4 to 6°C by 750 m depth.

Specimens of *Gnathophausia longispina* were collected at night during seven cruises of the NOAA ship "Townsend Cromwell" in 1984, 1985, 1987 and 1988. No *G. longispina* were collected during several daytime tows over the summit. All specimens in this study were collected with a 1.8 m Isaacs-Kidd midwater trawl (IKMT) with a 2.9 $m^2$ mouth opening. Mesh sizes for the net body and cod end varied among the early cruises: 10 and 0.333 mm (summer 1984), 3 and 3 mm (winter 1985, spring and summer 1987), and 3 and 0.505 mm (subsequent cruises), respectively. Net damage required the use of a replacement 5 mm-mesh net body during the last half of the winter 1988 cruise. All tows in 1984–1985 targeted the seamount-associated sound-scattering layer over the summit (Wilson and Boehlert 1990). Tows during spring 1987 were oblique to depths of 80 to 275 m. However, only two of these tows were deeper than 225 m in areas near the seamount where *G. longispina* were thought to occur, and thus may have under-sampled large specimens (see "Results"). Tows on subsequent cruises were either horizontal across the summit at nominal depths of 50, 100, 150, and 200 m, or oblique, generally to 250 m depth. The average ship speed during the IKMT tows was 1 to 2 m $s^{-1}$. Usually, IKMT tows were about 1 h long, although some shorter tows were made during the first three cruises. The volume of water filtered was determined with a calibrated General Oceanics flowmeter. The net depth profile was determined with a Benthos time–depth recorder during all IKMT tows except during the first two cruises, when net depth was estimated by the cosine of surface wire angle and meters of wire out.

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*Gnathophausia longispina* from all tows were immediately removed from the net and placed in about 4% buffered formaldehyde–seawater solution and later transferred to a 50% isopropanol–freshwater solution during subsequent processing in the laboratory. Specimens from summer 1984 and winter 1985 were only used to determine estimates of size-specific fecundity (i.e., brood size); specimens from later cruises were used to generate these and other biological results.

Carapace length (CL), from the eye to the posterior lateral edge of the carapace, was measured to the nearest 0.1 mm for random subsamples of at least 40 brooding females captured in the summers of 1984 (early July), 1987, and 1988 (late-August), fall 1988, winter 1985, and spring 1987 (only 3 specimens carrying young were caught in spring). For the 1987–1988 cruises, CL was determined for all *Gnathophausia longispina* from tows with fewer than about 75 specimens, or from a subsample ($n \geq 50$ individuals) for larger catches. To facilitate comparisons with other studies, CL and total length (TL) from the hind margin of the eye orbit to the posterior edge of the uropods and telson excluding the setae (Mauchline 1980) were measured for 74 specimens to determine the functional relationship between the two variables. The least-squares regression equation is $TL = 2.09 \cdot CL + 3.54$ ($r^2 = 0.99$). Measurements of *G. longispina* for the TL to CL sample and size-specific fecundity estimates were made with vernier calipers. Other CL measurements were made with a dissecting scope that was interfaced to a video-digitizing system (Optical Pattern Recognition System, Biosonics, Inc., Seattle, Washington).

Brooding females ($n = 181$) were grouped into 0.5 mm CL size classes to estimate size-specific fecundity (i.e., brood size). Counts included Stage I "egg-like" embryos, Stage II "eyeless" embryos, and Stage III "eyed" embryos, as defined by Mauchline (1980). Within each size class, the female with the greatest number of young within the marsupium was considered the best estimate of that size-specific fecundity. Justification for this assumption was the presence of many loose embryos of *G. longispina* in our samples, indicating that the young were often released from the marsupium upon capture and sample fixation. Only 22% ($n = 232$) of the brooding females (marsupium fully developed) actually carried young, based on samples from a subset of seven representative tows. Other mysids have been reported to release their young upon capture (Clutter 1967, Childress and Price 1978, Mauchline 1980, Carleton and Hamner 1989). Thus, maximum fecundity within each size interval was regressed on size by using weights equal to the interval sample size.

The CL and stage of sexual maturity for specimens possessing secondary sexual characters were recorded from deep (maximum net depth, $\geq 225$ m) and shallow ($\leq 125$ m) tows during the summers of 1987 and 1988 and all spring 1987 tows. Brooding females were considered to comprise Mauchline's (1980) Categories e–g; namely, mature females with (1) fully developed marsupium not yet filled with young, (2) ovigerous, and (3) "empty" females. Although the latter two categories were reasonably distinct, the former was not [as Mauchline (1980) also reported], and may have resulted in the inclusion of a few immature specimens. Likewise, our classification of males as sexually mature, on the basis of elongation of the spine on the posterior lobe of the pleuron of the second abdominal segment (Clarke 1962), is probably not perfect for smaller specimens, but was considered useful in the absence of any histological data on reproductive stages.

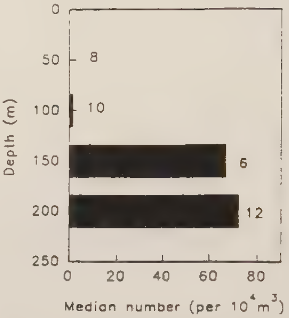

**Fig. 1.** *Gnathophausia longispina*. Vertical nighttime distribution over Southeast Hancock Seamount; data pooled from summer 1987 and summer, winter, and fall 1988. Number of tows is shown at end of each bar

**Table 1.** Cruises to Southeast Hancock Seamount, total number of *Gnathophausia longispina* caught, and number of tows in which species was present ($n$)

| Cruise | Dates | Total catch | Positive tows ($n$) |
|---|---|---|---|
| Summer 1984 | 07 July –30 July | 1 229 | 11 |
| Winter 1985 | 30 Jan. –25 Feb. | 831 | 12 |
| Spring 1987 | 11 Apr. –28 Apr. | 751 | 11 |
| Summer 1987 | 08 Aug. –25 Aug. | 1 173 | 18 |
| Winter 1988 | 12 Jan. –30 Jan. | 861 | 7 |
| Summer 1988 | 13 July –21 Aug. | 4 203 | 18 |
| Fall 1988 | 26 Oct. –08 Nov. | 2 059 | 15 |

## Results

A total of 11 107 *Gnathophausia longispina* were taken in IKMT sampling over Southeast Hancock Seamount during the course of the study (Table 1). Tows were not suitably stratified to produce abundance estimates for *G. longispina* at the seamount, but did demonstrate their patchy distribution over the summit. For example, Lloyd's (1967) index of patchiness (L) was 3.8 based on oblique summit IKMT tows. Catches from all tows ranged from 0 to 784 individuals per $10^4$ $m^3$ of water filtered.

Catches of *Gnathophausia longispina* from horizontal tows were greatest below 100 m depth (i.e., within ~100 m above the summit; Fig. 1). A total of only four specimens in eight tows (two tows per cruise) were taken at the 50 m depth interval. Vertical distribution patterns were similar among cruises.

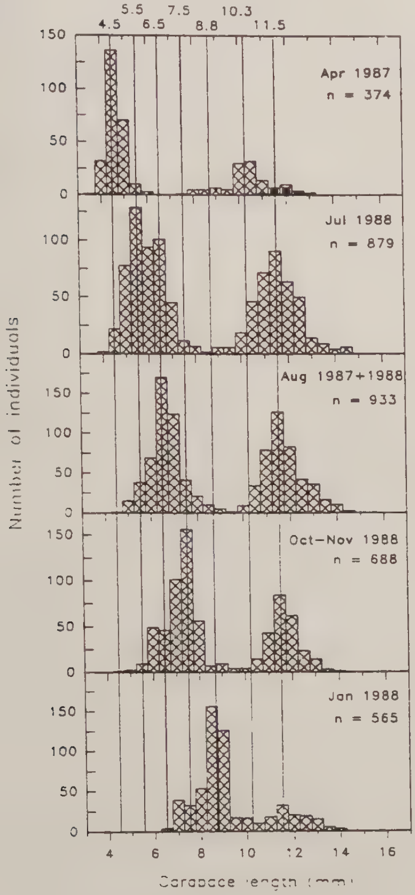

**Fig. 2.** *Gnathophausia longispina*. Size composition, as a function of month, regardless of year of collection. During summer 1988, tows were made in mid-July and again in mid-August. August samples from 1987 and 1988, which were similar, were combined. Seven vertical lines indicate modal lengths of presumed instar stages (see "Results"). Number of brooding females (filled bars) within each size class is shown for April

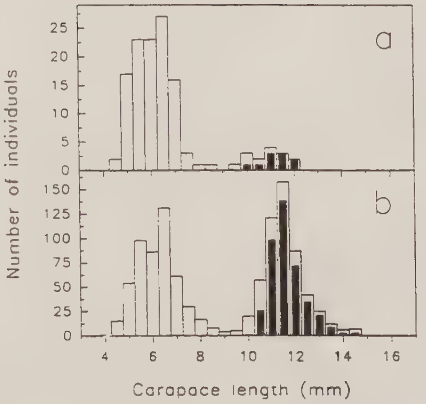

**Fig. 3.** *Gnathophausia longispina*. Size composition as a function of depth, for pooled data from summer of 1987 and 1988. Plots based on data from (a) tows <125 m depth ($n=128$ individuals) and (b) oblique tows from surface to >225 m depth ($n=1\,045$ individuals). Number of brooding females within each size class is shown by filled bars

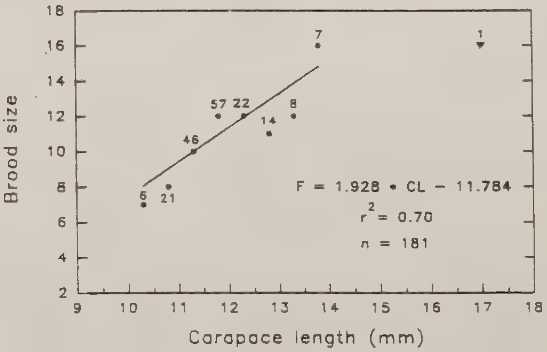

**Fig. 4.** *Gnathophausia longispina*. Maximum number of embryos in marsupium as function of carapace length. Fitted regression line was weighted by sample size (see "Results"); numbers above data points are sample sizes. ▼: Brood size of single specimen reported in Clarke (1962) (plotted for comparison only and not used in regression analysis)

The 3439 specimens of *Gnathophausia longispina* comprising the carapace length sample ranged from 3.7 (spring 1987) to 14.7 mm CL (male and female specimen, summer 1988). Length–frequency plots from each cruise were bimodal (Fig. 2). When plots were arranged by month without regard to year of collection, progression of the smaller mode to larger sizes was clearly apparent over time (Fig. 2). However, no similar increase was observed for the larger mode, which remained around 11.5 mm CL regardless of season.

When the bimodal length data from the summer of 1987 and 1988 cruises were combined and plotted as a function of depth, relatively greater numbers of small individuals were found at shallow depths (Kolmogorov-Smirnov test, $P<0.001$; Fig. 3). Thus, the population size-composition of *Gnathophausia longispina* from the nominal 0 to 250 m depth comprised about equal numbers in the two dominant length modes of ~6.5 and 11.5 mm CL (Fig. 3b), whereas relatively few large specimens occurred above 125 m depth (Fig. 3a). No trends in size with depth were observed during spring 1987 and winter and fall 1988 (data not shown). The sex ratio of those specimens from the summers of 1987 and 1988 with developed secondary sexual characteristics was 3.3 females : 1 male.

Among the 0.5 mm CL categories, the maximum number of brooding embryos increased with size of the ovigerous female and equaled 7 to 16 (Fig. 4). Size classes contained 6 to 57 brooding females. A simple linear relationship between maximum fecundity (F) and CL of the

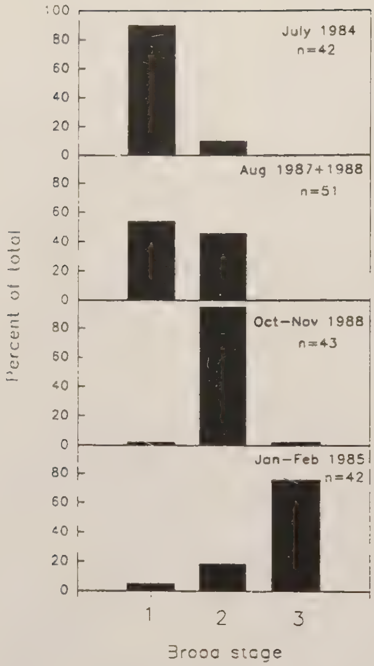

Fig. 5. *Gnathophausia longispina*. Percent carrying Stage I, II, and III embryos from early summer (July 1984), late summer (August 1987 and 1988), fall (October–November 1988), and winter (January–February 1985). Only three females carrying embryos were captured during spring (April 1987); these are not included

brooding female was considered most descriptive. The fitted regression equation was $F = 1.928 \cdot CL - 11.784$ ($r^2 = 0.70$). The smallest *Gnathophausia longispina* actually brooding embryos was 10.1 mm CL (3 Stage I embryos, summer 1984), and the largest was 14.0 mm CL (16 Stage I embryos, summer 1987). The smallest male with a slightly elongated pleural spine on the second abdominal segment was 8.4 mm CL (spring 1987), although most specimens were at least 10 mm CL (mean CL = 11.2 mm, SD = 1.19, $n = 136$).

Development of *Gnathophausia longispina* embryos through Stages I–III takes about 7 to 9 mo, with parturition occurring in late winter–early spring. Embryos from ovigerous *G. longispina* were typically in the same developmental stage during any given season (Fig. 5). During early summer (July 1984), 90% of the females with young carried Stage I embryos. By late summer (August of 1987 and 1988), females with young carried either Stage I (54%) or Stage II (46%) embryos. By fall, 95% of the females with young carried Stage II embryos, and by winter (1985), 76% carried Stage III embryos. During spring (April 1987), only three females carried young: two at Stage III (11.5 and 12.9 mm CL) and one at Stage I (12.3 mm CL). Thus, most brooding females were carrying Stage I embryos in July and probably released young between February and April.

The sizes of the Stage I or Stage III embryos did not appear to differ with the size of the brooding female. The mean diameter of Stage I embryos from a small (10.1 mm CL) brooding female was 2.4 mm (SD 0.07, $n = 3$) and from a large (13.8 mm CL) brooding female was 2.3 mm (SD 0.14, $n = 11$). Mean body length (from base of eyestalk) of Stage III embryos from three small ($\leq 11.0$ mm CL) brooding females was 7.8 mm (SD 0.81, $n = 7$) and from the three large ($\geq 12.9$ mm CL) females was 7.9 (SD 0.85, $n = 15$).

## Discussion

A large population of *Gnathophausia longispina* is a persistent feature associated with Southeast Hancock Seamount. The occurrence of large numbers of *G. longispina* at different stages of development, during various seasons, and among different years (Table 1, Fig. 2) suggest that development of all growth stages regularly occurs at the seamount. The patchy distribution of *G. longispina* in our samples is probably related to aggregating behavior, which has been linked with population retention in other mysids (O'Brien 1988). Euphausiid patchiness is greater near shallow topography (L = 5.0) than in the open ocean (L = 2.6), but this is probably related to disruption of the normal pattern of distribution by current–topography interactions or predation (Genin et al. 1988).

Recruitment of *Gnathophausia longispina* to the seamount probably depends on local processes rather than immigration, as no other large aggregations of *G. longispina* have been reported along the southern Emperor–northern Hawaiian Ridge (SE–NHR). *G. longispina* were not taken during a survey we conducted over four other seamounts along the SE–NHR in 1988 (summer). Although *G. longispina* were reported farther south off the main Hawaiian Islands as early as the late 1800's (Clarke 1962), a recent study (Reid et al. 1991) around the islands found maximum catches of less than ~7 individuals per $10^4$ $m^3$ of water filtered. Population maintenance of seamount-associated species such as *G. longispina* probably relies on various physical and biological mechanisms, and their aggregating behaviour may play an important role, as in other mysids (Clutter 1969, O'Brien 1988, Kaartvedt 1989).

An analysis of the length–frequency histograms provides the first estimates of growth for *Gnathophausia longispina* over intermediate instar stages. The temporal progression of the smaller length mode in the size–frequency histograms among seasons suggests that modal lengths may represent successive instars and can thus provide estimates of growth over these stages (Fig. 2). Although a wide variation in molt factor and synchronized breeding could produce a similar temporal progression of modal length, the narrow size ranges observed within seasons suggest that modal lengths probably represent different instar stages. Similarly discrete size classes in *G. ingens* have been verified as different instar stages (Childress and Price 1978). Thus, we tentatively refer to each size class in the length distribution as representing a particular instar stage. Based on the vertical lines fitted by eye to the length data in Fig. 2 to identify modal positions of the various presumed instars, seven instar stages are probably represented in the data. The bimodal size–frequency data from July presumably represent three instar stages (Fig. 2). Assuming the percentage increase in CL with size to be roughly constant, the smaller length–frequency mode in July is about equally composed of two instars: a younger instar stage centered at a modal length of ~5.5 mm CL, and an older instar at ~6.5 mm CL.

Reduction in growth with the onset of sexual maturity is common in crustaceans (Somerton 1980), and probably occurs in *Gnathophausia longispina*. The length mode at 11.5 mm CL (Fig. 2) probably represents the instar stage at sexual maturity, and possibly a terminal molt, since it persists as the largest mode in the data and generally defines the length range of brooding females (Fig. 3). Non-brooding individuals composed nearly the entire 10.3 mm CL length mode, which preceded the 11.5 mm CL mode, and was present in April (Fig. 2). (Insufficient sampling effort below the 225 m depth interval during April probably resulted in the relatively small number of specimens within the 10.3 mm CL size class.) The size distribution of the fecundity sample (mean 11.8 mm CL; Fig. 4) was similar to the 11.5 mm CL modal size distribution in the length samples (Fig. 2); this also suggests that production of young occurs at the latter instar stage.

Growth of *Gnathophausia longispina* is estimated at about 0.015 mm CL $d^{-1}$ (Table 2) when determined over the period beginning with the earliest instar stage (April, 4.5 mm CL modal length) and ending with the first appearance of the large temporally stationary mode centered at 11.5 mm CL (July; Fig. 2). Growth of sexually mature individuals (11.5 mm CL mode) either slows dramatically or ceases altogether (Fig. 2). Estimates of growth are similar when determined using the first (April) and last (July) instar stages, or those instars separated by shorter time intervals (Table 2).

**Table 2.** *Gnathophausia longispina*. Estimates of growth in carapace length (CL) based on analysis of length–frequency histograms in Fig. 2 (see "Results" for further details). "start" and "end" identify approximate collection dates of the two length samples used to estimate growth. $\Delta t$: number of days between start and end time midpoints; $\Delta L$: difference between the two modal CLs associated with start and end times. Location of modal CLs of different presumed instar stages are indicated by seven vertical lines in Fig. 2. Entries below dashed line are growth estimates over shorter time intervals that suggest relatively constant growth over these instar stages

| Time | | $\Delta t$ | $\Delta L$ (mm) | Growth (mm $d^{-1}$) |
|---|---|---|---|---|
| start | end | | | |
| Apr. | July | 457 | 11.5–4.5<br>7.0 | 0.015 |
| Apr. | Apr. | 365 | 10.3–4.5<br>5.8 | 0.016 |
| Apr. | Jan. | 274 | 8.8–4.5<br>4.3 | 0.016 |
| Apr. | July[a] | 92 | >5.5–4.5<br>1.0 | >0.011 |
| | | | <6.5–4.5<br>2.0 | <0.022 |
| Aug. | Oct./Nov. | 76 | 7.5–6.5<br>1.0 | 0.013 |
| Oct.–Nov. | Jan. | 77 | 8.8–7.5<br>1.3 | 0.017 |
| Jan. | Apr. | 91 | 10.3–8.8<br>1.5 | 0.016 |
| Apr. | July | 92 | 11.5–10.5<br>1.2 | 0.013 |

[a] We assumed that the smaller length mode in July (Fig. 2) was composed of two modes (two instar stages) centered at 5.5 and 6.5 mm CL. Thus, $\Delta L$ between April and July was intermediate between 1 (5.4 minus 4.5) and 2 (6.5 minus 4.5) mm CL. Likewise, $\Delta L$ between July and August (not shown) was probably <1 (6.5 minus 5.5) mm CL, since roughly half of the smaller individuals were already ~6.5 mm CL in July

As is common in many Crustacea (Mauchline 1977) including *Gnathophausia ingens* (Childress and Price 1978), molt increments for *G. longispina* – represented by the difference in modal length pairs of successive instars – decreased with an increase in size. Considering the seven length modes (Fig. 2), molt increment (expressed as a percentage of the previous instar CL) was 22% for April–July, 18% for July–August, 15% for August–October, 17% for October–January, 17% for January–April, and 12% for April, and the largest CL mode was in July. For *G. ingens*, molt increments similarly decreased from about 25% at the second free-living stage to 12% when sexual maturity was reached (Childress and Price 1978).

Although a positive relationship between the number of young in the marsupium and female size is common in shallow-dwelling mysid species, it is less apparent among meso- and bathypelagic species (Mauchline 1973, Wittmann 1984). However, Childress and Price (1983) found a strong relationship between embryo number and size of the brooding parent for *Gnathophausia ingens* when sufficient specimens had been collected. Based on a single brooding female taken near the Equator (5°54′N; 162°05′W), Clarke (1962) suggested that the number of embryos carried in the marsupium of *G. longispina* varied little from the 16 "eggs" found in his specimen. Mauchline (1972: Table 4; 1980: Table 3) listed a maximum brood size of 1 for *G. longispina*.

The number of young *Gnathophausia longispina* in the marsupium increased with the size of the brooding female (Fig. 4). No *G. longispina* specimens as large as the brooding female reported by Clarke (1962) have been collected at Southeast Hancock Seamount. However, if our derived relationship between maximum observed fecundity and CL for *G. longispina* is representative of other geographic locations, then specimens of the size reported by Clarke may carry as many as 21 embryos (versus his observed value of 16 young; Fig. 4). Thus, brood size in *G. longispina* may range from ~7 in small females to as high as 16 (and possibly 21) in large specimens. Given that some growth stages of *G. longispina* were stratified by depth (Fig. 3) and little sampling occurred within 50 m above the summit or flanks at Southeast Hancock

Seamount, larger specimens of the size reported by Clarke may concentrate in this region near the seamount. At deeper depths (560 to 640 m) around the Hawaiian Islands (Ortmann 1903), *G. longispina* have a median CL of 14 mm (range 5 to 17 mm CL from six reported lengths), which exceeds the largest length mode we recorded at Southeast Hancock (Fig. 2) and approaches the larger CL in Clarke (Fig. 4). Two other aspects of the life history of *G. longispina* reported by Clarke should be revised in view of our data. He reported the minimum size of sexual maturity for female *G. longispina*, based on the only available specimen, as 17 mm CL (40 mm TL). The smallest female with eggs from our study had a 10 mm CL (24 mm TL). He also reported that *G. longispina* occur as shallow as 150 m depth. Although most individuals from our study were from this depth or greater, a few were from 50 m.

Evaluation of the results from this present study suggests the following life-history pattern for *Gnathophausia longispina*. A single brood is produced annually, with young released from the marsupium in late winter–early spring at a size of ~2.1 mm CL (8 mm TL). In addition to the length data for free-living *G. longispina* (Fig. 2) and near-term embryos, this pattern is suggested by the nearly synchronous development of embryos among all brooding females over the course of at least 7 mo (Fig. 5). The youngest free-living instars, although not collected in the samples, are likely to be present during the late winter between January and April and undergo two molts [assuming 25% growth increment as reported for *G. ingens* in Childress and Price (1978) to reach the earliest instar represented in Fig. 2 (i.e., about 4.5 mm CL)]. These first two free-living stages probably occur close to the substrate, where no samples were taken. Although these relatively abundant early stages would easily have passed through the net (particularly that used during spring 1987), we would have expected a few in the fine-mesh cod end if they had been present well above the summit during other times of the year. Growth of the young over the size ranges represented by our samples (Fig. 2) continues throughout the year, with most reaching sexual maturity within 12 to 15 mo after birth at a size of about 11.5 mm CL (Figs. 2 and 3). By late winter or spring, few adults (11.5 mm modal CL, Fig. 2) remain in the population, although increased sampling effort below the 225 m depth is needed to verify this (see "Materials and methods"). Thus, the entire life-span of *G. longispina* at Southeast Hancock Seamount is about 2 yr.

A decrease in growth with increasing latitude by *Gnathophausia longispina* may explain the large specimens reported by Ortmann (1903) and Clarke (1962) which were discussed earlier. Alternatively, *G. longispina* (unlike *G. ingens* which are semelparous and carry their young at a single instar; Childress and Price 1978) may survive beyond the end of their second year of life to reside at greater depths than were sampled in the present study. This pattern is also suggested by the rather large size range of ovigerous *G. longispina* at Southeast Hancock Seamount (10 to 14 mm CL). However, no bimodal length distributions of brooding females were observed from April 1987 (Fig. 2), pooled August of 1987 and 1988 (Fig. 3), or size-specific fecundity samples (Fig. 4; distribution not shown), which would indicate the presence of two year-classes. Nevertheless, it is possible that a large reduction in growth accompanying sexual maturity caused CLs of successive instars to coalesce into the unimodal size distribution at 11.5 mm CL (Fig. 2), a situation that has been observed in other crustaceans (e.g. *Gennadas elegans*; Mauchline 1991).

Both *Gnathophausia longispina* and the deeper-dwelling congener *G. ingens* (Childress and Price 1978, 1983) show similarities in life-history patterns, some of which are characteristic of other meso- and bathypelagic mysids (Mauchline 1991). Larger individuals (e.g. brooding females) typically occur deeper for both species, and brood periods are long – about 17 mo for *G. ingens* and 7 mo for *G. longispina*. Although *G. longispina* are much smaller and thus exhibit about half the absolute growth rate of *G. ingens* [0.030 mm CL $d^{-1}$ from Fig. 4 in Childress and Price (1978)], the relative growth rate (absolute, expressed as percentage of mean CL of population) of *G. longispina* (0.20% $d^{-1}$) is about twice that of *G. ingens* (0.11% $d^{-1}$). Both species exhibit similar decreases in CL growth increments over their life span, particularly at the stage where sexual maturity is reached. Finally, results of the present work suggest that *G. longispina* has slightly fewer free-living instar stages than *G. ingens* (~9 vs 13). Additional sampling closer to the bottom, particularly during late winter–early spring, as well as developmental studies to positively identify different instars of *G. longispina*, will be helpful to further clarify this aspect of the species' life history, as well as to confirm a 2 yr life span for this species.

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# Comparing Dynamic Versions of the Schaefer and Fox Production Models and Their Application to Lobster Fisheries

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Dynamic approaches (integrated and finite difference) to the Schaefer and Fox production models are applied to four commercial lobster fisheries. The integrated versions provided better predictions than their finite difference counterparts. Only the integrated version of the Fox model provides realistic (positive) biological parameter estimates for all four fisheries, and bootstrapping reveals those estimates to be generally stable. Additionally, this model performs well when applied to data where certain assumptions of surplus production modeling are fulfilled. The results suggest further investigation of the integration procedure.

Des méthodes dynamiques (méthode intégrée et méthode des différences finies) sont appliquées aux modèles de production de Schaefer et de Fox dans le cas de quatre pêches commerciales au homard. Les versions utilisant la méthode intégrée permettent d'obtenir de meilleures prévisions par rapport aux versions fondées sur la méthode des différences finies. Seule la version intégrée du modèle de Fox fournit des estimations réalistes (valables) des paramètres biologiques pour les quatre pêches, et l'application de la technique du *bootstrapping* démontre que ces estimations sont généralement stables. En outre, on obtient de bons résultats lorsque l'on applique ce modèle aux données qui confirment certaines hypothèses relativement aux modèles de production excédentaire. Ces résultats incitent donc à pousser les recherches du côté de la méthode intégrée.

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One of the simplest approaches to modeling a fishery is applying a surplus production model to a time series of catch and effort data. Schaefer (1957) and Fox (1970) helped pioneer this approach and used the concept of equilibrium to model a fishery over the long run. They first applied a dynamic model to estimate various biological parameters of a fishery. The parameters were then used in an equilibrium model to estimate fishery management parameters (e.g. maximum sustainable yield). The dynamic models therefore had a dual purpose: to account for the nonequilibrium portions of a fishery and to accurately estimate the biological parameters so the resulting management parameters could be trusted. Many authors (Walter 1973; Schnute 1977; Uhler 1980; Lleonart and Salat 1989) have since developed their own dynamic versions of the Schaefer (1957) and Fox (1970) models to better assess unstabilized fisheries. The two dynamic approaches examined in this paper are the original (finite difference) versions and the integrated versions (Schnute 1977; Clarke et al. 1992).

The Schaefer (1957) and Fox (1970) models have the continuous forms

$$(1) \quad dX/dt = rX - rX^2/K - C$$

and

$$(2) \quad dX/dt = rX \ln(K/X) - C,$$

respectively, where $X$ represents the population, $dX/dt$ the growth rate of the population, $C$ the catch rate, $r$ the intrinsic growth rate, and $K$ the maximum stock level or virgin biomass. Equation (1) assumes that the growth rate to biomass relationship is logistic (parabolic), while Equation (2) assumes a Gompertz distribution (Richards 1959).

Fishing effort is taken into consideration by substituting $C = qEX$, with $q$ defined as the catchability coefficient and $E$ as the rate of fishing effort (e.g. the effort expended in 1 yr). Equations (1) and (2) are then converted to

$$(3) \quad (1/U)dU/dt = r - r/(qK)U - qE$$

and

$$(4) \quad (1/U)dU/dt = r \ln(qK) - r \ln(U) - qE,$$

respectively, where $U = C/E$ is the instantaneous catch per unit effort (CPUE). Schaefer (1957) and Fox (1970) estimated parameters $r$, $q$, and $K$ by converting Equations (3)and (4) into their finite difference forms:

Schaefer:

$$(5) \quad \Delta U_n/U_n = r - r/(qK)U_n - qE_n$$

Fox:

$$(6) \quad \Delta U_n/U_n = r \ln(qK) - r \ln(U_n) - qE_n$$

where $U_n$ is the average CPUE and $E_n$ is the total effort expended for year $n$ and $\Delta U_n = (U_{n+1} - U_{n-1})/2$. Both Equations (5) and (6) are considered dynamic given that $U_{n+1}$ can be expressed in terms of past variables $U_n$, $E_n$, and $U_{n-1}$. Originally, Equations (5) and (6) were used only to estimate parameters $r$, $q$, and $K$. However, we test the applicability of the dynamic models for predictions and parameter estimation in nonequilibrium conditions. Hereafter, Equations (5) and (6) will be called the FD (finite difference) - Schaefer and FD-Fox models, respectively.

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Upon scrutiny, the FD-Schaefer and FD-Fox models possess some questionable properties. One problem is the approximation $dU/dt = \Delta U_n$, which assumes that CPUE is linearly distributed over the course of 2 yr. Another problem is that the CPUE of year $n + 1$, $U_{n+1}$, can be predicted without the anticipated effort being specified for that year. Such a condition is questionable, given the definition of CPUE: $U = C/E$.

Rather than using a finite difference approximation, Schnute (1977) integrated Equation (3) and approximated the average annual CPUE as the geometric mean of the instantaneous CPUEs at the beginning and end of the year. Schnute's dynamic version of the Schaefer model, henceforth referred to as the Schnute model, is

$$(7) \quad \ln (U_{n+1}/U_n) = r - (r/(qK)) (U_n + U_{n+1})/2 - q(E_n + E_{n+1})/2.$$

As noted by Uhler (1980), the Schnute model, unlike the FD-Schaefer and FD-Fox models, has the desirable property that $U_{n+1}$ tends to zero as $E_{n+1}$ becomes large. Another advantage of this model is that the predicted CPUE, $U_{n+1}$, can be estimated for a range of anticipated effort, $E_{n+1}$, to allow fishery managers to approximate the effort level needed for a targeted yield. In Uhler (1980), the Schnute model was shown to have less bias than an FD-Schaefer model (with a 1-yr time lag) when applied to a computer-simulated fishery.

An integrated version of the Fox model has been applied to the lobster fishery in the Northwestern Hawaiian Islands (NWHI) (Clarke et al. 1992). This model uses the same assumptions as the Schnute model and incorporates a Taylor series approximation (Appendix A):

$$(8) \quad \ln(U_{n+1}) = [2r \ln(qK) + (2 - r) \ln(U_n) - q(E_n + E_{n+1})]/(2 + r).$$

Unlike the other models presented, this model is a simple, lagged logarithmic equation of CPUE. This gives the model an advantage over the Schnute and finite difference models when regression analysis is performed. This model has been applied to a limited time series of catch and effort data (8 yr of the NWHI lobster fishery: Clarke et al. 1992), but its applicability to fisheries with longer time series is unknown. Hereafter, this model will be called the I (integrated) - Fox model.

Our paper examines the assumption that the integrated models will yield better predictions and biological parameter estimates than the finite difference models. The models are applied to four commercial lobster fisheries with substantial time series of catch and effort data, and each model's ability to predict annual CPUE is investigated. Biological parameter estimates for each fishery also are presented. However, since little is known of these parameters, only general conclusions are made about them. Each model's ability for parameter estimation is tested using data sets in which the biological parameter $q$ is known.

## Methods

A frequently used approach to estimate a model's predictive power of catch is applying an ordinary least squares (OLS) regression on all years of data for a fishery. The points on the resulting regression curve are then interpreted as catch (or CPUE) predictions for the original data. Wittink (1988) pointed out that this approach depends heavily on the $R$-squared ($R^2$) value and does not test for predictive power, since the regression curve is created using the original data (i.e. the curve has prior knowledge of what it is supposed to predict).

The approach used in this paper is to make annual predictions only using data prior to that year. Mathematically, OLS is performed on the first $m - 1$ years of data, and a prediction is made for year $m$ using the results of that regression. A regression is then performed on the first $m$ years for the prediction of year $m + 1$, and this procedure is continued until a prediction is made for the last year of available data. The predicted and actual values are then compared to determine predictive power. This approach better approximates what fishery managers actually face because having data for future years is unrealistic.

Each model's estimates of the biological parameters $r$, $q$, and $K$, using all years of data for a fishery, are also examined. From definitions presented in Schnute (1977), each biological parameter should be positive. The parameter estimates presented in our paper are unconstrained estimates. Other papers (e.g. Schaefer 1957) take absolute values to ensure the analyses have realistic (positive) results. We use the unconstrained approach to look at the mathematical relations of the models rather than to thoroughly analyze a specific fishery.

The four dynamic models are applied to catch and effort data from four lobster fisheries: Western Australian rock lobster, *Panulirus cygnus* (years 1944–64 from table 1 in Morgan 1979a; years 1965–78 from tables 6 and 8 in Morgan et al. 1982); American lobster, *Homarus americanus* (years 1950–79 from table 1 in Townsend 1986); Tasmanian rock lobster, *Jasus novaehollandiae* (years 1947–84 from table 1 in Campbell and Hall 1988); and New Zealand lobster, *Jasus edwardsii* (years 1945–90 from the totals in table 1 in Breen 1991). The Western Australian data take into account seasonal variability and area distribution (Morgan 1979b). The New England data are only inshore data, and a modified Schaefer model was applied to them in Townsend (1986). An FD-Fox model and an FD-Schaefer model with 1-yr time lags have been applied to the Tasmanian data (Campbell and Hall 1988). Finally, the New Zealand data are composed of the total of commercial and estimated unreported, amateur, and illegal catch data. To our knowledge, each data set has not been proven to satisfy all assumptions of surplus production modeling. However, the applicability of these models to commercial data can be gauged by each model's ability to forecast catch (or CPUE).

A prediction for the CPUE of year $m + 1$ is made in the following manner. An OLS regression is applied to the models by using catch and effort data for the first $m$ years of a fishery. The resulting regression on data for years $n = 1$ to $n = m$ estimates the parameters $r$, $q$, and $K$:

FD-Schaefer:

$$(9) \quad \Delta U_{n-1}/U_{n-1} = c1 + c2U_{n-1} + c3E_{n-1}$$

with $r = c1$, $q = -c3$, and $K = -r/(qc2)$;

FD-Fox:

$$(10) \quad \Delta U_{n-1}/U_{n-1} = c1 + c2 \ln(U_{n-1}) + c3E_{n-1}$$

with $r = -c2$, $q = -c3$, and $K = e^{c1/r}/q$;

Schnute:

$$(11) \quad \ln(U_n/U_{n-1}) = c1 + c2(U_{n-1} + U_n)/2 + c3(E_{n-1} + E_n)/2$$

with $r = c1$, $q = -c3$, and $K = -r/(qc2)$; and

I-Fox:

$$(12)\quad \ln(U_n) = c1 + c2\ln(U_{n-1}) + c3(E_{n-1} + E_n)$$

with $r = 2(1 - c2)/(1 + c2)$, $q = -c3(2 + r)$, and $K = e^{c1(2+r)/(2r)}/q$. The FD-Schaefer and FD-Fox models predict the following year's CPUE with

FD-Schaefer:

$$(13)\quad U_{m+1} = U_{m-1} + 2U_m[r - r/(qK)\,U_m - qE_m]$$

and

FD-Fox:

$$(14)\quad U_{m+1} = U_{m-1} + 2U_m[r\ln(qK) - r\ln(U_m) - qE_m].$$

For the I-Fox model, after the anticipated effort $E_{m+1}$ is specified, the predicted CPUE is

$$(15)\quad U_{m+1} = e^{\frac{(2r\ln(qK) + (2-r)\ln(U_m) - q(E_m + E_{m+1}))}{(2+r)}}.$$

For the Schnute model, $U_{m+1}$ was estimated from Equation (31) in Schnute (1977). Confidence intervals for the Schnute model's prediction are in Schnute (1977); those for the I-Fox are in Appendix B.

The predictive ability of the models is tested by using Theil's $U$-statistic (Wittink 1988):

$$(16)\quad U_T = \sqrt{\frac{\sum_{n=k}^{N}(U_n - U_{p,n})^2}{\sum_{n=k}^{N}(U_n - U_{n-1})^2}}$$

where $U_{p,n}$ is the predicted CPUE for year $n$, and $k$ and $N$ are equal to the first and last year, respectively, that a CPUE prediction was made. The numerator of $U_T$ is the sum of the squared differences of the actual and predicted CPUEs, and the denominator is the sum of the squared differences between the actual CPUEs of adjacent years. Thus, this statistic adjusts a model's predictive error by considering the year-to-year variation of the actual CPUE. If $U_T > 1$, the model is not considered useful for forecasting purposes.

For the overall estimation of biological parameters ($r$, $q$, and $K$), the following procedure is used. First, regressions of the four models are performed on all years of data. The presence of autocorrelation is then investigated. Since the I-Fox model has a lagged dependent variable, the Durbin–Watson statistic is inappropriate to detect autocorrelation, and the test statistic used is the Durbin $h$-statistic (Pindyck and Rubinfeld 1981). When the Durbin $h$-statistic is undefined, the Durbin $t$-statistic test is applied (King 1987). If the FD-Schaefer, FD-Fox, or Schnute model passes either the Durbin $h$-test or the regular Durbin–Watson test, then the results of that model's regression are used. When evidence of autocorrelation is detected, the Cochrane–Orcutt procedure for autocorrelation correction (Wittink 1988) is applied until the model's test statistic is not significant in showing autocorrelation. The model loses a degree of freedom for each Cochrane–Orcutt iteration performed.

TABLE 1. Average percent prediction errors from the I-Fox, Schnute, FD-Fox, and FD-Schaefer models for four lobster fisheries.

| Location | I-Fox | Schnute | FD-Fox | FD-Schaefer |
|---|---|---|---|---|
| New England | 11.58 | 10.35 | 18.56 | 18.56 |
| New Zealand | 18.86 | 16.58 | 20.92 | 20.62 |
| Tasmania | 12.20 | 12.26 | 21.54 | 21.01 |
| Western Australia | 12.49 | 12.75 | 25.69 | 24.26 |

TABLE 2. Theil's $U$-statistic test applied to the I-Fox, Schnute, FD-Fox, and FD-Schaefer models for four lobster fisheries.

| Location | I-Fox | Schnute | FD-Fox | FD-Schaefer |
|---|---|---|---|---|
| New England | 0.780[a] | 0.750[a] | 1.44 | 1.43 |
| New Zealand | 1.86 | 3.20 | 2.46 | 2.43 |
| Tasmania | 0.827[a] | 0.910[a] | 1.60 | 1.55 |
| Western Australia | 1.01 | 1.21 | 2.70 | 2.45 |

[a] Model is considered an adequate predictor.

## Results and Discussion

The lack of degrees of freedom for regression analysis with the FD-Fox and FD-Schaefer models, which have a 2-yr time lag, prevented predictions from being made for the first 6 yr of each fishery. Therefore, CPUE predictions for years 1956–79, 1951–90, 1953–84, and 1950–78 were obtained for the New England, New Zealand, Tasmanian, and Western Australian lobster fisheries, respectively. A model's CPUE prediction for the seventh year used the regression results from the first 6 yr of data, the prediction for the eighth year used those from the first 7 yr of data, and so on.

The percent prediction error

$$(17)\quad 100\,|U_n - U_{p,n}|/U_n$$

was calculated for each model's prediction of CPUE, with $U_{p,n}$ being the predicted CPUE for year $n$. The means of the percent prediction errors from each model (Table 1) show that the I-Fox model is the most accurate predictor for two of the four fisheries, and the Schnute model is the more accurate predictor for the other two. In all four fisheries, the I-Fox and Schnute models have lower average percent prediction errors than the finite difference models. According to Theil's $U$-statistic test (Table 2), the I-Fox and Schnute models are adequate predictors for the Tasmanian and New England fisheries, while the FD-Fox and FD-Schaefer models failed the test for all four fisheries.

From the regressions on all data of a fishery, only the I-Fox model provides positive biological parameters for all four fisheries (Tables 3–6). The I-Fox model also had high $R^2$ values (>0.8), but this goodness of fit was expected. The low $R^2$ values from the other three models reveal problems in explaining the variation in their more complex dependent variables ($\Delta U_n/U_n$ for the FD-Fox and FD-Schaefer models and $\ln(U_{n+1}/U_n)$ for the Schnute model) over substantially long time series. This was probably a major reason for their unrealistic (negative) estimates of the biological parameters. Another possible explanation is that the data sets examined do not satisfy the assumptions of surplus production modeling. The higher $R^2$ values of the I-Fox model compared with those of the Schnute model reveal that a better regression fit does not necessarily imply better predictive power (Ferber 1956).

Bootstrapping (Efron and Tibshirani 1986) was applied to the I-Fox model to test the stability of the biological parameters. Sampling with replacement was applied to the residuals of each

TABLE 3. Final regression coefficients and parameter estimates for the New England inshore lobster fishery (NA = not applicable). $^*P < 0.05$.

| | I-Fox | Schnute | FD-Fox[a] | FD-Schaefer[a] |
|---|---|---|---|---|
| $c1$ | −1.62 | −0.444 | 0.399 | −0.308 |
| $t$-ratio for $c1$ | −2.57* | −1.40 | 0.742 | −1.11 |
| $c2$ | 0.416 | 7.94 | 0.176 | 4.68 |
| $t$-ratio | 1.79 | 1.28 | 0.911 | 0.830 |
| $c3$ | $-2.41 \times 10^{-4}$ | $1.61 \times 10^{-4}$ | $1.75 \times 10^{-4}$ | $1.15 \times 10^{-4}$ |
| $t$-ratio for $c3$ | −2.42* | 1.26 | 1.07 | 1.04 |
| df | 26 | 26 | 24 | 24 |
| $R^2$ | 0.943 | 0.0606 | 0.0493 | 0.0439 |
| $R^2$ adj | 0.939 | −0.0117 | −0.0299 | −0.0358 |
| Durbin $h$ | Undefined | Undefined | Undefined | Undefined |
| Durbin $t$ | 1.32* | NA | NA | NA |
| Durbin–Watson | 1.19 | 1.95* | 1.69* | 1.70* |
| $r$ ($\text{yr}^{-1}$) | 0.826 | −0.444 | −0.176 | −0.308 |
| $q$ ($1000 \text{ traps}^{-1}$) | $6.80 \times 10^{-4}$ | $-1.61 \times 10^{-4}$ | $-1.75 \times 10^{-4}$ | $-1.15 \times 10^{-4}$ |
| $K$ (millions of pounds) | 92.6 | −347 | −591 | −571 |

[a] One iteration of the Cochrane–Orcutt procedure was applied.

TABLE 4. Final regression coefficients and parameter estimates for the New Zealand inshore lobster fishery (NA = not applicable). $^*P < 0.05$.

| | I-Fox[a] | Schnute[b] | FD-Fox | FD-Schaefer |
|---|---|---|---|---|
| $c1$ | 0.369 | −0.0773 | −0.0446 | −0.0523 |
| $t$-ratio for $c1$ | 2.18* | −0.539 | −0.366 | −0.464 |
| $c2$ | 0.718 | 0.0158 | 0.0165 | 0.00875 |
| $t$-ratio for $c2$ | 6.06* | 0.391 | 0.192 | 0.281 |
| $c3$ | $-4.24 \times 10^{-5}$ | $2.01 \times 10^{-6}$ | $-1.30 \times 10^{-6}$ | $-1.58 \times 10^{-6}$ |
| $t$-ratio for $c3$ | −2.41* | 0.0902 | −0.0502 | −0.0870 |
| df | 40 | 41 | 41 | 41 |
| $R^2$ | 0.934 | 0.0108 | 0.00974 | 0.0108 |
| $R^2$ adj | 0.930 | −0.0374 | −0.0386 | −0.0375 |
| Durbin $h$ | −1.05* | −0.163* | 1.31* | 1.09* |
| Durbin–Watson | NA | 2.05* | 1.68* | 1.68* |
| $r$ ($\text{yr}^{-1}$) | 0.329 | −0.0773 | −0.0165 | −0.0523 |
| $q$ ($1000 \text{ pot-lifts}^{-1}$) | $9.88 \times 10^{-5}$ | $-2.01 \times 10^{-6}$ | $1.30 \times 10^{-6}$ | $1.58 \times 10^{-6}$ |
| $K$ (tonnes) | 37 469 | −2 440 845 | 11 527 340 | 3 788 069 |

[a] Two iterations of the Cochrane–Orcutt procedure were applied.
[b] One iteration of the Cochrane–Orcutt procedure was applied.

TABLE 5. Final regression coefficients and parameter estimates for the Tasmanian lobster fishery (NA = not applicable). $^*P < 0.05$.

| | I-Fox | Schnute | FD-Fox | FD-Schaefer |
|---|---|---|---|---|
| $c1$ | 6.40 | 0.494 | 1.34 | 0.272 |
| $t$-ratio for $c1$ | 5.41* | 1.36 | 0.978 | 1.03 |
| $c2$ | 0.256 | $-1.14 \times 10^{-4}$ | −0.162 | $-6.64 \times 10^{-5}$ |
| $t$-ratio for $c2$ | 1.89 | −1.66 | −1.02 | −1.29 |
| $c3$ | −0.416 | −0.311 | −0.135 | −0.174 |
| $t$-ratio for $c3$ | −4.30* | −1.11 | −0.660 | −0.889 |
| df | 34 | 34 | 33 | 33 |
| $R^2$ | 0.833 | 0.0953 | 0.0452 | 0.0624 |
| $R^2$ adj | 0.823 | 0.0421 | −0.0126 | 0.00556 |
| Durbin $h$ | 0.976* | −1.35* | 5.46 | 1.52* |
| Durbin–Watson | NA | 2.44 | 1.44 | 1.49 |
| $r$ ($\text{yr}^{-1}$) | 1.19 | 0.494 | 0.162 | 0.272 |
| $q$ ($\text{million pot-days}^{-1}$) | 1.33 | 0.311 | 0.135 | 0.174 |
| $K$ (tonnes) | 4079 | 13 997 | 29 056 | 23 467 |

of the four I-Fox data sets (a Cochrane–Orcutt-transformed data set was used for the New Zealand fishery), and a regression was performed on each new data set. This procedure was replicated 1000 times with each regression yielding new estimates of $r$, $q$, and $K$. The mean, standard deviation, and coefficient of variation of the $r$, $q$, and $K$ bootstrap estimates for each fishery are shown in Table 7. The coefficients of variation suggest that the parameters derived from the I-Fox model are relatively stable for all parameters except $K$ (high variability was shown in the New England and New Zealand lobster fisheries).

The integrated models predict CPUE reasonably (<20% error) for all four lobster fisheries but fail to pass Theil's $U$-

TABLE 6. Final regression coefficients and parameter estimates for the Western Australian lobster fishery (NA = not applicable). $^*P < 0.05$.

| | I-Fox | Schnute | FD-Fox[a] | FD-Schaefer[a] |
|---|---|---|---|---|
| $c1$ | 0.617 | 0.106 | −0.284 | −0.411 |
| $t$-ratio for $c1$ | 3.73* | 0.304 | −1.42 | −1.58 |
| $c2$ | 0.429 | −0.0369 | 0.209 | 0.127 |
| $t$-ratio for $c2$ | 2.88* | −0.297 | 1.22 | 1.41 |
| $c3$ | −0.0354 | −0.0113 | 0.032 | 0.0332 |
| $t$-ratio for $c3$ | −3.67* | −0.410 | 1.33 | 1.51 |
| df | 31 | 31 | 29 | 29 |
| $R^2$ | 0.882 | 0.00725 | 0.0572 | 0.0735 |
| $R^2$ adj | 0.875 | −0.0568 | −0.00781 | 0.00955 |
| Durbin $h$ | 1.58* | 0.144* | 2.58 | 0.608* |
| Durbin–Watson | NA | 1.97* | 1.78* | 1.81* |
| $r$ (yr$^{-1}$) | 0.799 | 0.106 | −0.209 | −0.411 |
| $q$ (million pot-lifts$^{-1}$) | 0.0991 | 0.0113 | −0.0317 | −0.0332 |
| $K$ (millions of kilograms) | 29.7 | 253 | −123.4 | —98.0 |

[a] One iteration of the Cochrane–Orcutt procedure was applied.

TABLE 7. Bootstrap estimates of the means, standard deviations (SD), and coefficients of variation (CV) of parameter $r$, $q$, and $K$ when applying the I-Fox model to four lobster fisheries.

| Parameter | Mean | SD | CV |
|---|---|---|---|
| | *New England* | | |
| $r$ | 0.912 | 0.509 | 0.56 |
| $q$ | 0.000755 | 0.000430 | 0.57 |
| $K$ | 120.2 | 399.8 | 3.33 |
| | *New Zealand* | | |
| $r$ | 0.340 | 0.170 | 0.50 |
| $q$ | 0.000102 | 0.0000513 | 0.50 |
| $K$ | 44 061 | 96 482 | 2.19 |
| | *Tasmania* | | |
| $r$ | 1.23 | 0.368 | 0.30 |
| $q$ | 1.38 | 0.469 | 0.34 |
| $K$ | 4355 | 1573 | 0.36 |
| | *Western Australia* | | |
| $r$ | 0.838 | 0.316 | 0.38 |
| $q$ | 0.103 | 0.0400 | 0.39 |
| $K$ | 33.7 | 18.6 | 0.55 |

statistic for the New Zealand and Western Australian fisheries. Also, despite providing positive, unconstrained estimates of the biological parameters, instability with the I-Fox model is shown in parameter $K$. These findings could indicate a theoretical problem with all of the models investigated: the assumption that $C = qEX$. Since the estimates of biomass are not known, verification of this assumption is difficult. However, data sets designed to fit this assumption exist. The applicability of the I-Fox model toward these data sets is explored.

## Application to the Silliman and Gutsell (1958) Data Sets

Guppy populations (*Lebistes reticulatus*) were introduced into four similarly designed tanks, and two (called populations A and B) were "fished" with a certain percent removal during each 3-wk interval (Silliman and Gutsell 1958). Fishing effort data were computed so that $U = qX$ with $q = 0.1$. Since two tanks were unfished, the maximum stock level each tank achieved could be thought of as estimates of the virgin biomass $K$. The maximum weight attained in tanks C and D equaled 37.1 and 36.0 g, respectively. This suggests that reasonable estimates of $K$ for populations A and B are probably in the range of 30–40 g. Pella and Tomlinson (1969) estimated $q = 0.071$ and $K = 49.3$ for population A and $q = 0.078$ and $K = 39.5$ for population B.

Tables 8 and 9 present the catch and effort data along with estimates of $q$, $K$, and predicted CPUE $U_p$ from the I-Fox model for each 3-wk interval. The catch data are from Silliman and Gutsell 1958) whereas the effort data are adjusted by scaling the percent weight removals as suggested in Pella and Tomlinson (1969). Each estimate of $q$, $K$, and $U_p$ is obtained from the I-Fox regression on all data prior to that 3-wk interval. Because of a lack of degrees of freedom, the I-Fox regression estimates could not be obtained for the first four observations of each table.

The tables present some revealing points of the I-Fox model. For example, the initial estimates of $q$ and $K$ are unrealistic (negative). This could be due either to the lack of data or to the effort levels for the first 13 observations being in a narrow range. Also, despite obtaining negative values of $q$ and $K$, the I-Fox model still predicted CPUE accurately. This implies that a model that estimates biological parameters poorly could still prove useful when predicting future catch (e.g. the Schnute model applied to the New England lobster fishery). Finally, the I-Fox model's estimates become unrealistic for the last observations, suggesting that the model encounters problems when applied to fisheries nearing extinction.

The main point of the tables is that the I-Fox model accurately assesses "fisheries" A and B for a large portion of their life spans. In both populations, estimates of $q$ and $K$ become fairly stable by week 100, with the estimates of population B hovering around the "true" values of $q$ (0.1) and $K$ (between 30 and 40). Considering the I-Fox model is an adequate predictor of CPUE (Theil's $U$-statistic was 0.751 for population A and 0.781 for population B), the model seems to be a valuable management tool for fisheries that satisfy the assumption of $C = qEX$.

The ability of the other three models to estimate parameter $q$ has also been analyzed. As was done in Tables 8 and 9 with the I-Fox model, values of $q$ were obtained from each model (Fig. 1). The deviation of each $q$ estimate from 0.100,

TABLE 8. Predicted CPUE $U_p$, prediction error, and parameters $K$ and $q$ from the I-Fox model for each 3-wk interval in the population A data set of Silliman and Gutsell (1958).

| Week | Catch | Effort | CPUE | $U_p$ | % error | $K$ | $q$ |
|---|---|---|---|---|---|---|---|
| 40 | 6.0 | 2.58 | 2.33 | | | | |
| 43 | 4.9 | 2.49 | 1.97 | | | | |
| 46 | 3.7 | 2.06 | 1.80 | | | | |
| 49 | 4.4 | 2.50 | 1.76 | | | | |
| 52 | 4.1 | 2.43 | 1.69 | 1.82 | 7.69 | −2.9 | −0.326 |
| 55 | 3.5 | 2.15 | 1.63 | 1.68 | 3.07 | 30.1 | 0.072 |
| 58 | 3.5 | 2.32 | 1.51 | 1.63 | 7.95 | 35.6 | 0.058 |
| 61 | 3.8 | 2.59 | 1.47 | 1.51 | 2.72 | −98.5 | −0.014 |
| 64 | 3.3 | 2.36 | 1.40 | 1.45 | 3.57 | 41.0 | 0.049 |
| 67 | 3.3 | 2.23 | 1.48 | 1.40 | 5.41 | 31.5 | 0.099 |
| 70 | 2.8 | 1.90 | 1.47 | 1.52 | 3.40 | 26.5 | 0.131 |
| 73 | 3.0 | 2.00 | 1.50 | 1.50 | 0.00 | 31.0 | 0.079 |
| 76 | 3.9 | 2.62 | 1.49 | 1.49 | 0.00 | 31.5 | 0.077 |
| 79 | 1.4 | 1.05 | 1.33 | 1.52 | 14.29 | 31.5 | 0.076 |
| 82 | 2.1 | 1.41 | 1.49 | 1.29 | 13.42 | −15.5 | −0.064 |
| 85 | 1.9 | 1.23 | 1.54 | 1.53 | 0.65 | 39.4 | 0.050 |
| 88 | 2.0 | 1.33 | 1.50 | 1.58 | 5.33 | 37.7 | 0.054 |
| 91 | 1.7 | 1.06 | 1.60 | 1.53 | 4.38 | 51.1 | 0.035 |
| 94 | 1.5 | 0.90 | 1.67 | 1.64 | 1.80 | 40.0 | 0.049 |
| 97 | 1.9 | 1.06 | 1.79 | 1.69 | 5.59 | 37.6 | 0.054 |
| 100 | 1.7 | 0.97 | 1.75 | 1.81 | 3.43 | 34.2 | 0.067 |
| 103 | 1.2 | 0.62 | 1.94 | 1.79 | 7.73 | 35.0 | 0.062 |
| 106 | 2.0 | 0.94 | 2.13 | 1.96 | 7.98 | 33.2 | 0.075 |
| 109 | 2.0 | 0.87 | 2.30 | 2.14 | 6.96 | 35.5 | 0.084 |
| 112 | 2.6 | 1.12 | 2.32 | 2.31 | 0.43 | 42.3 | 0.089 |
| 115 | 2.9 | 1.23 | 2.36 | 2.29 | 2.97 | 43.2 | 0.089 |
| 118 | 3.0 | 1.31 | 2.29 | 2.32 | 1.31 | 47.0 | 0.089 |
| 121 | 11.2 | 4.77 | 2.35 | 1.95 | 17.02 | 45.3 | 0.089 |
| 124 | 7.0 | 4.58 | 1.53 | 1.91 | 24.84 | 88.7 | 0.063 |
| 127 | 5.2 | 4.37 | 1.19 | 1.21 | 1.68 | 51.6 | 0.097 |
| 130 | 5.7 | 5.09 | 1.12 | 0.95 | 15.18 | 52.8 | 0.098 |
| 133 | 5.6 | 5.05 | 1.11 | 0.93 | 16.22 | 40.3 | 0.088 |
| 136 | 4.2 | 4.38 | 0.96 | 1.00 | 4.17 | 36.7 | 0.079 |
| 139 | 4.3 | 4.78 | 0.90 | 0.89 | 1.11 | 37.2 | 0.080 |
| 142 | 3.5 | 4.32 | 0.81 | 0.85 | 4.94 | 37.0 | 0.080 |
| 145 | 3.9 | 5.42 | 0.72 | 0.76 | 5.56 | 38.2 | 0.080 |
| 148 | 3.5 | 5.00 | 0.70 | 0.67 | 4.29 | 39.7 | 0.080 |
| 151 | 3.4 | 6.54 | 0.52 | 0.63 | 21.15 | 38.3 | 0.080 |
| 154 | 2.1 | 7.00 | 0.30 | 0.44 | 46.67 | 42.8 | 0.082 |
| 157 | 2.4 | 7.27 | 0.33 | 0.24 | 27.27 | 71.3 | 0.084 |
| 160 | 1.2 | 6.32 | 0.19 | 0.30 | 57.89 | 39.3 | 0.092 |
| 163 | 1.2 | 6.67 | 0.18 | 0.17 | 5.56 | 71.8 | 0.083 |
| 166 | 0.9 | 6.92 | 0.13 | 0.16 | 23.08 | 60.5 | 0.087 |
| 169 | 1.0 | 7.14 | 0.14 | 0.11 | 21.43 | 91.9 | 0.080 |
| 172 | 0.2 | 3.33 | 0.06 | 0.15 | 150.00 | 59.7 | 0.088 |

$|q - 0.1|$, was then computed for each 3-wk interval after week 82 (the last week that the models estimated a negative value of q). The average deviations for each model reveal that the integrated models are superior to the finite difference models in estimating $q$. For population A, the average deviations for the I-Fox and Schnute models are 0.024 and 0.029, respectively. The FD-Fox and FD-Schaefer models estimate $q$ more poorly; the average deviation is 0.043 for each model. For population B, the I-Fox and Schnute models estimate $q$ more accurately, with average deviations of 0.012 and 0.013, respectively. Although the FD-Schaefer and FD-Fox models are also more accurate in population B than in population A (0.030 and 0.033 average deviations, respectively), their $q$ estimates are still not as accurate as the integrated models.

## Conclusion

Ideally, fishery managers require a model that accurately predicts catch (or CPUE) while also estimating reasonable biological parameters. None of the models performed exceptionally well when applied to the four commercial lobster data sets, although a case could be made for the applicability of the I-Fox model to the Tasmanian lobster fishery. The model passed Theil's $U$-statistic when predicting CPUE and had positive (and stable) biological parameters. Yet specific instances of inaccurate CPUE predictions by the I-Fox model were still found. This supports the consensus that surplus production models are too simple to accurately reflect fish and fishery interactions. Temperature, spawning stock information, and operational

TABLE 9. Predicted CPUE $U_p$, prediction error, and parameters $K$ and $q$ from the I-Fox model for each 3-wk interval in the population B data set of Silliman and Gutsell (1958).

| Week | Catch | Effort | CPUE | $U_p$ | % error | $K$ | $q$ |
|---|---|---|---|---|---|---|---|
| 40 | 8.0 | 2.60 | 3.08 | | | | |
| 43 | 5.0 | 2.13 | 2.35 | | | | |
| 46 | 5.6 | 2.55 | 2.20 | | | | |
| 49 | 5.6 | 2.86 | 1.96 | | | | |
| 52 | 4.5 | 2.57 | 1.75 | 1.89 | 8.00 | 12.0 | 0.417 |
| 55 | 4.0 | 2.50 | 1.60 | 1.84 | 15.00 | 14.4 | 0.453 |
| 58 | 3.1 | 2.18 | 1.42 | 1.61 | 13.38 | 24.8 | 0.142 |
| 61 | 3.5 | 2.57 | 1.36 | 1.35 | 0.74 | −12.0 | −0.053 |
| 64 | 3.5 | 2.63 | 1.33 | 1.32 | 0.75 | −15.7 | −0.046 |
| 67 | 3.7 | 2.50 | 1.48 | 1.30 | 12.16 | −14.4 | −0.049 |
| 70 | 3.6 | 2.45 | 1.47 | 1.44 | 2.04 | −9.6 | −0.078 |
| 73 | 3.4 | 2.30 | 1.48 | 1.43 | 3.38 | −10.7 | −0.074 |
| 76 | 3.8 | 2.70 | 1.41 | 1.46 | 3.55 | −18.6 | −0.052 |
| 79 | 1.5 | 1.13 | 1.33 | 1.36 | 2.26 | −18.5 | −0.051 |
| 82 | 1.9 | 1.22 | 1.56 | 1.22 | 21.79 | −8.7 | −0.084 |
| 85 | 1.9 | 1.17 | 1.62 | 1.65 | 1.85 | 30.4 | 0.083 |
| 88 | 2.1 | 1.30 | 1.62 | 1.68 | 3.70 | 31.2 | 0.078 |
| 91 | 2.3 | 1.42 | 1.62 | 1.64 | 1.23 | 33.3 | 0.067 |
| 94 | 2.2 | 1.26 | 1.75 | 1.64 | 6.29 | 34.0 | 0.064 |
| 97 | 1.9 | 1.02 | 1.86 | 1.77 | 4.84 | 31.8 | 0.074 |
| 100 | 2.3 | 1.10 | 2.09 | 1.89 | 9.57 | 30.7 | 0.083 |
| 103 | 2.4 | 1.09 | 2.20 | 2.09 | 5.00 | 30.3 | 0.098 |
| 106 | 2.8 | 1.24 | 2.26 | 2.18 | 3.54 | 31.1 | 0.104 |
| 109 | 2.7 | 1.14 | 2.37 | 2.23 | 5.91 | 31.9 | 0.107 |
| 112 | 3.3 | 1.39 | 2.37 | 2.32 | 2.11 | 33.7 | 0.111 |
| 115 | 1.9 | 0.89 | 2.13 | 2.36 | 10.80 | 34.5 | 0.112 |
| 118 | 2.2 | 1.02 | 2.16 | 2.19 | 1.39 | 31.9 | 0.107 |
| 121 | 10.2 | 4.66 | 2.19 | 1.85 | 15.53 | 31.8 | 0.106 |
| 124 | 7.0 | 4.70 | 1.49 | 1.67 | 12.08 | 38.2 | 0.086 |
| 127 | 6.8 | 5.62 | 1.21 | 1.13 | 6.61 | 33.8 | 0.105 |
| 130 | 5.3 | 5.64 | 0.94 | 0.95 | 1.06 | 34.1 | 0.097 |
| 133 | 4.3 | 4.67 | 0.92 | 0.81 | 11.96 | 34.1 | 0.098 |
| 136 | 4.8 | 4.80 | 1.00 | 0.86 | 14.00 | 32.1 | 0.094 |
| 139 | 4.2 | 4.94 | 0.85 | 0.93 | 9.41 | 30.5 | 0.092 |
| 142 | 3.5 | 5.07 | 0.69 | 0.81 | 17.39 | 30.9 | 0.094 |
| 145 | 2.6 | 4.81 | 0.54 | 0.68 | 25.93 | 32.5 | 0.095 |
| 148 | 2.8 | 4.52 | 0.62 | 0.54 | 12.90 | 38.0 | 0.092 |
| 151 | 3.7 | 6.98 | 0.53 | 0.57 | 7.55 | 33.7 | 0.096 |
| 154 | 2.9 | 6.44 | 0.45 | 0.46 | 2.22 | 34.6 | 0.097 |
| 157 | 1.2 | 6.00 | 0.20 | 0.42 | 110.00 | 34.8 | 0.097 |
| 160 | 1.7 | 7.73 | 0.22 | 0.17 | 22.73 | 64.6 | 0.092 |
| 163 | 1.1 | 8.46 | 0.13 | 0.18 | 38.46 | 42.7 | 0.101 |
| 166 | 0.3 | 6.00 | 0.05 | 0.12 | 140.00 | 54.9 | 0.101 |
| 169 | 0.2 | 10.00 | 0.02 | 0.03 | 50.0 | $4.6 \times 10^{44}$ | 0.071 |

changes should be incorporated to better approximate the dynamics of a fishery. Both integrated models, however, show adequate predictive power for the four lobster fisheries and estimate $q$ accurately for the Silliman and Gutsell (1958) data sets. We believe that as mentioned in Silliman (1971), surplus production models can be valuable as first approximations and should be considered in time- or data-limiting conditions.

More sophisticated nonlinear approaches to the FD-Schaefer, FD-Fox, and Schnute models are found in Pella and Tomlinson (1969), Fox (1975), and Schnute (1977), respectively. These observation error fitting procedures (Hilborn and Walters 1992) use an iterative procedure with a least squares criterion to obtain estimates of $r$, $q$, and $K$ which minimize predictive error. The parameters obtained from the linear models examined here are first approximations to that criterion. Using simulated populations, Hilborn (1979) showed that the nonlinear FD-Schaefer and Schnute models produced positive parameters, while their linear counterparts gave negative results; however, the nonlinear methods were not shown to assess those fisheries any better than the linear methods. A nonlinear approach applied to the I-Fox model could possibly produce better results, but this is beyond the scope of the current study. A more complete discussion on the inclusion of a model's observed error structure is found in Schnute (1989).

The present paper has compared two linear dynamic approaches with the Schaefer and Fox production models. The results suggest that the integration approach of Schnute (1977) should be explored more extensively. For example, the integration procedure could incorporate a longer time lag (Walter 1973) to account for the recruitment patterns of lobster. A 4-yr period was shown to work for the Western Australian lobster fishery in Phillips (1986). Additionally, the integration approach could be applied to a more general class of curves, such as the Bernoulli curves used in Pella and Tomlinson (1969), with the chosen curve satisfying some statistical criterion. Research in these areas could lead to a better under-

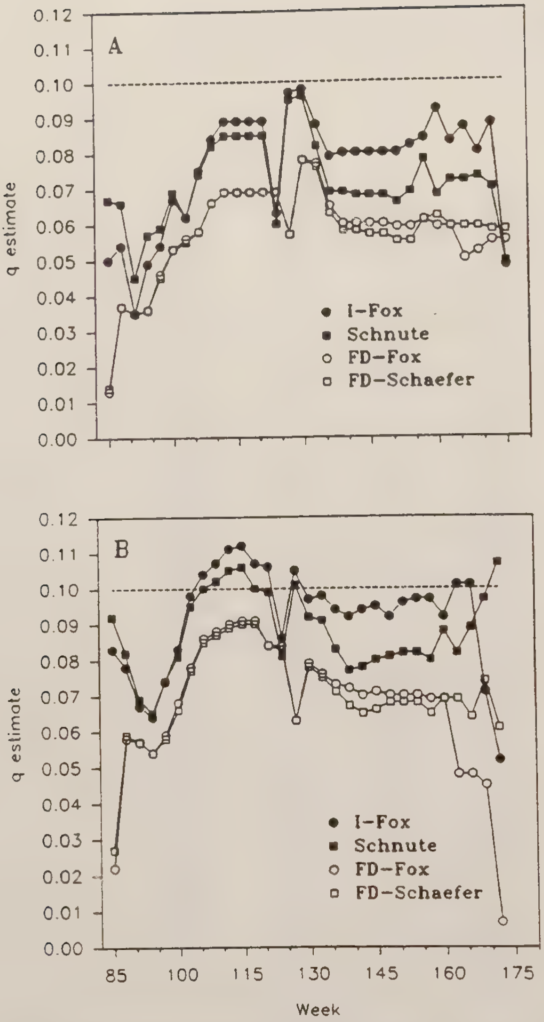

FIG. 1. Estimates of *q* obtained from the I-Fox, Schnute, FD-Fox, and FD-Schaefer models for the population (A and B) data sets of Silliman and Gutsell (1958)

standing of the relative usefulness of surplus production modeling in specific fishery applications.

## Acknowledgements

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## Appendix A. Derivation of the I-Fox Model

Integrating Equation (4) from $t$ = year $n$ to $t$ = year $n + 1$ yields

$$\text{(A1)}\quad \ln(U\langle n+1\rangle / U\langle n\rangle) = r\ln(qK) - r\int_{t=n}^{n+1} \ln(U)\,dt - qE_n$$

where $U\langle n\rangle$ is the instantaneous CPUE at the start of year $n$ and $E_n$ is the total effort for year $n$.

The first-degree Taylor polynomial for $\ln(U)$ centered at $U_n$, the average CPUE for year $n$, is

$$\begin{aligned}\ln(U) &\approx \ln(U_n) + (1/U_n)(U - U_n) \\ &= \ln(U_n) - 1 + (U/U_n).\end{aligned}$$

This approximation assumes that $U$ will not fluctuate far from $U_n$ over the course of year $n$. Thus, high variability of instantaneous CPUE due to seasonal effects may render this assumption (and the I-Fox model) invalid for a specific fishery.

Integration of the Taylor approximation yields

$$\text{(A2)}\quad \int_n^{n+1} \ln(U)\,dt = \ln(U_n) - 1 + (1/U_n)\int_n^{n+1} U dt.$$

By definition, $U_n = \int_n^{n+1} U dt$, so Equation (A2) becomes

$$\int_n^{n+1} \ln(U)\,dt = \ln(U_n) - 1 + 1 = \ln(U_n).$$

Putting this result into Equation (A1) gives

$$\ln(U < n+1 > / U < n >) = r\ln(qK) - r\ln(U_n) - qE_n.$$

Adding this equation to its corresponding $(n + 1)$th equation gives

$$\begin{aligned}\text{(A3)}\quad &\ln((U\langle n+2\rangle\, U\langle n+1\rangle)/(U\langle n+1\rangle\, U\langle n\rangle)) \\ &= 2r\ln(qK) - r(\ln(U_{n+1}) + \ln(U_n)) - q(E_n + E_{n+1}).\end{aligned}$$

Schnute's (1977) assumption is used to estimate instantaneous CPUE:

$$U_n = \sqrt{U\langle n+1\rangle\, U\langle n\rangle},$$

that is, the CPUE of a given year is the geometric mean of the CPUEs at the beginning and ending of that year. Using this CPUE estimate in Equation (A3) and solving algebraically for $\ln(U_{n+1})$ gives

$$\begin{aligned}\ln(U_{n+1}) = {} & (2r/(2 + r))\ln(qK) + ((2 - r)/(2 + r)) \\ & \ln(U_n) - (q/(2 + r))(E_n + E_{n+1}).\end{aligned}$$

## Appendix B. Confidence Intervals for the I-Fox Model's Prediction of Catch per Unit Effort

The standard error of forecast $S_f$ for the I-Fox model's prediction of CPUE for year $m + 1$ is found by applying the procedure in Ezekiel and Fox (1959):

$$S_f = \sqrt{S_1^2\left(1 + \frac{1}{m-1} + c_{XX}(X_m - M_X)^2 + 2c_{XY}(X_m - M_X)(Y_m - M_Y) + c_{YY}(Y_m - M_Y)^2\right)}$$

where $X_n = \ln(U_n)$, $Y_n = E_n + E_{n+1}$, $Z_n = \ln(U_{n+1})$, $M_X = \Sigma X_n/(m - 1)$, $M_Y = \Sigma Y_n/(m - 1)$, $S_X = \Sigma(X_n - M_X)^2$, $S_Y = \Sigma(Y_n - M_Y)^2$, $S_{XY} = \Sigma(X_n - M_X)(Y_n - M_Y)$, $c_{XX} = S_Y/(S_X S_Y - S_{XY}^2)$, $c_{XY} = -S_{XY}/(S_X S_Y - S_{XY}^2)$, $c_{YY} = S_X/(S_X S_Y - S_{XY}^2)$, $S_1^2 = \Sigma(Z_n - c1 - c2X_n - c3Y_n)^2/(m - 4)$, and $m$ is the number of years of data used. All sums $(\Sigma)$ are from $n = 1$ to $n = m - 1$, and $c1$, $c2$, and $c3$ are the regression coefficients of the I-Fox regression. Also, the number of degrees of freedom is $m - 4$ because of the 1-yr time lag.

Using the formula for $S_f$, a confidence interval for $\ln(U_{m+1})$ can be calculated:

Lower limit: $l = \ln(U_{m+1}) - S_f\, t_{p/2}$

and

Upper limit: $u = \ln(U_{m-1}) + S_f\, t_{p/2}$

where $t_{p/2}$ is the critical value of the Student's $t$-distribution statistic of $p/2$ probability.

Since the natural log function $\ln(U)$ is an increasing function and is well defined for $U > 0$, confidence limits for the prediction $U_{m+1}$ can be estimated by taking the inverse (exponent) of the confidence limits for $\ln(U_{m+1})$:

Lower limit: $e^l$

and

Upper limit: $e^u$.

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# ROCKS AND FISHES: SUBMERSIBLE OBSERVATIONS IN A SUBMARINE CANYON

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*A multi-disciplinary study to assess the importance of small-scale refugia to species of large rockfishes in deep water was undertaken recently in Monterey Bay. Isolated rock habitat at depths suitable for rockfishes in Soquel Canyon (up to 300 m) was identified using fine-scale bathymetry and sidescan sonar imaging, verified with visual observations from a manned submersible, mapped and quantified. Species composition, size, and habitat specificity (type and depth) of fishes associated with these features were estimated using a video camera and parallel laser system along transects made from a submersible. High numbers of large (up to 1 m) rockfishes were locally associated with rock ledges, small caves, crevices, and overhangs. Two distinct assemblages of rockfishes were obvious from clustering analysis; small species were associated with mud and cobble substrata of low relief, while larger species were found under ledges or near large structures on vertical walls, ridges and boulder fields. Relative abundance and size of the largest species were higher and larger, respectively, when estimated from submersible surveys than from partyboat catch records from adjacent areas. We suggest that discontinuous rock outcrops of high relief are inaccessible fishing areas and thereby provide natural refuge for commercially and recreationally important fishes in Soquel Canyon.*

## INTRODUCTION

Rockfishes (Sebastes sp.) are heavily exploited in recreational and commercial fisheries along the west coast of the United States. These fisheries in California are worth over $1 billion, considering all associated industry, with recreational value far exceeding that of the commercial fisheries (Lenarz 1987). Rockfishes have been harvested continuously in California with various types of gear (e.g., hook and line, gill net, and trawl) since the early 1900's. Historically, rockfish landings have been especially high in Monterey (Phillips 1939).

Many species of rockfishes are slow-growing, long-lived, and older at maturity. Because of these life history characteristics, as well as patchy distributions and likely residentiality, local stocks of rockfishes are particularly vulnerable to over fishing. Indeed, decline in abundance and size of large species of rockfishes has been noted in recent recreational catches landed in the Monterey area. As local stocks within the bay become depleted, the Monterey fleet has expanded its range to greater distances from port.

Commercial and recreational fisheries can affect the sustainability of coastal rockfish populations by changing their distribution, abundance, and diversity. Accurate assessment of these factors is critical for effective management, protection, and restoration of this resource. Because California is considering the use of marine harvest refugia, and is in the process of designating four marine ecological reserves, it is important to identify and describe the extent of naturally-occurring refugia.

There is little information on the distribution, abundance, and other ecological characteristics of mature rockfishes associated with deep-water rocky habitat in the Monterey Bay area. This type of habitat is beyond SCUBA capabilities, and the rocky substrata prohibit accurate estimates of fish abundance using conventional trawl surveys. Despite this lack of knowledge, deep-water rocky features are important rockfish habitats. Using the submersible *Delta* for two exploratory dives in 1991, we observed high numbers of mature rockfishes and lingcod (Ophiodon elongatus) associated with an isolated rocky outcropping surrounded by a field of mud along the side of a submarine canyon in Monterey Bay. Our observations of species of large rockfishes in deepwater in the Monterey Bay submarine canyon system were somewhat surprising because they represent very low numbers in the hook and line fisheries in the area and are rarely observed during shallow water surveys by scuba divers. Geologists were likewise surprised at the incidence of such variable habitat in a canyon that was thought to be dormant and without the influence of erosion processes.

Our general objective is to assess rockfish resources and their potential habitat in the Monterey Bay submarine canyon system by combining geophysical techniques and submersible observations. Our working hypothesis is that rocky outcrops along the headward sides of these canyons serve as refugia for deep-dwelling rockfishes. We are evaluating rockfish species composition, abundance, and species-specific size distribution within heavily-fished and lightly-fished areas of the same depth and habitat. Because most of the shallow and more accessible rocky areas in Monterey Bay have been heavily fished continuously for most of this century, fishes in these areas expectedly would be fewer in number, smaller, and not yet reproductively active when compared with less accessible areas. Exposed rocky habitat in relatively deep water outside the depth range of recreational fishing could serve as spawning and birthing grounds for larger, and perhaps older individuals of some species, and may produce a significant number of recruits.

## METHODOLOGY

This represents preliminary findings during the first year of a multi-year study supported by NOAA National Underseas Research Program (NURP), and conducted by fisheries biologists from NOAA, National Marine Fisheries Service's Pacific Fisheries Environmental Group (PFEG), Moss Landing Marine Laboratories (MLML), the California Department of Fish and Game (CDFG), and the Marine Science Institute at University of California, Santa Barbara, and geologists from the U.S. Geological Survey (USGS) and MLML.

Our approach to assess rockfish assemblages and their habitat in inaccessible, lightly fished areas included three methodologies performed as three phases of the 1992 pilot study. First we conducted a survey of the bathymetry in our Soquel Canyon study site using a 3.5 kHz echo sounder integrated with Global Positioning System (GPS) navigational data along track lines. From this survey we produced a fairly fine-scale bathymetric map of the area (Fig. 1), with depth contours at only 20 m intervals. We identified areas of high relief and potential slumping, and used this map to select our submersible dive sites.

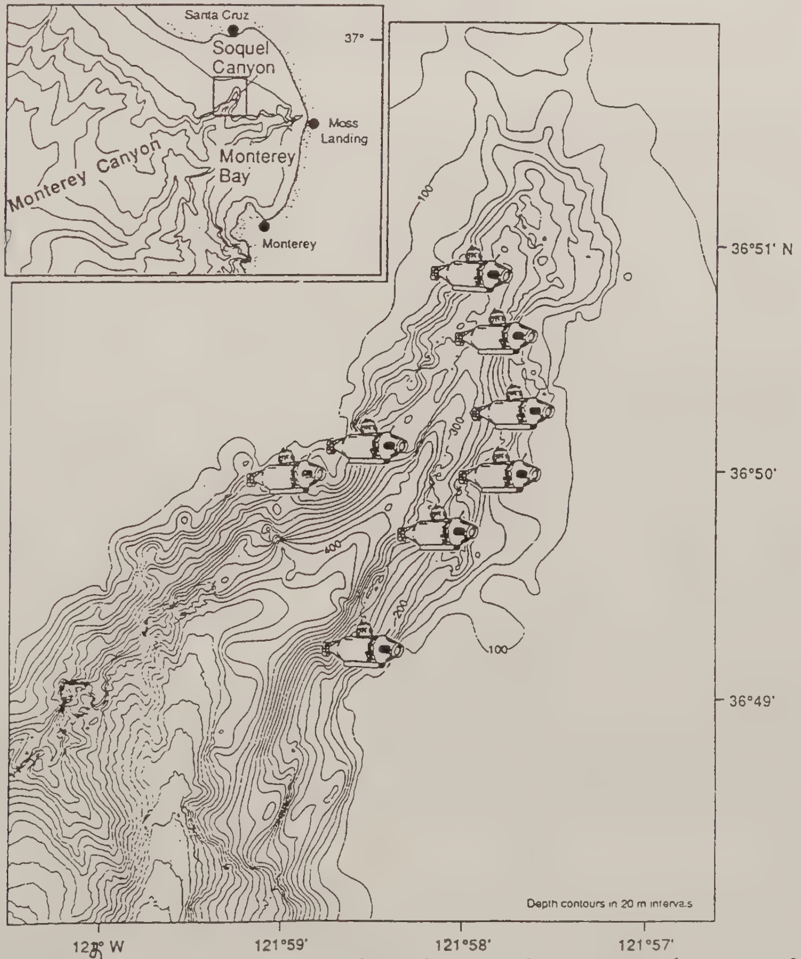
Santa Cruz
37°
Soquel Canyon
Moss Landing
Monterey Canyon
Monterey Bay
Monterey
36°51' N
36°50'
36°49'
100
300
400
200
100
Depth contours in 20 m intervals
122° W
121°59'
121°58'
121°57'

Figure. 1. Fine-scale (contours at 20 m intervals) bathymetric map of Soquel Canyon and sites of submersible dives.

During the second phase of our study, eight sites (Fig. 1) were evaluated as potential rockfish habitat using the *Delta* submersible in water from 80 to 305 m. at the head of the canyon. The *Delta* is a relatively small submersible, accommodating one scientific observer and one pilot, has a maximum operating depth of about 350 m, and a cruise speed of 1.5 knots. An acoustic track-point system on board the support vessel monitors the underwater location of the submersible. Most of the dives were made during daylight to avoid potential bias due to diel activity patterns of the fishes. Each dive was documented continuously with a high-8 mm video camera and associated lights that were externally mounted to the starboard side of the submersible; the scientific observer verbally annotated each video tape. A hand-held high-8 mm video camera and voice recorder were used as back-up data recorders. Divers de-briefed themselves after their dives, including transcribing observations on fishes and habitat from audio and video tapes into a computerized database on board the support vessel.

To quantify fish abundance and habitat use, belt transects (e.g., Pearcy et al. 1989, Stein et al. 1993) of 10-min duration were conducted 1-2 m from the bottom at 0.4-0.9 knots. In spite of recognized biases of visual transect techniques (i.e., effects of observer and lights, resighting mobile fishes, variable width of transect and field of view), belt transects are probably the most appropriate survey method considering the sedentary behavior of demersal rockfishes and the heterogeneity of their environment. Transects were purposely of short duration to maintain constant depth within the rock habitat at each station. All fishes in front of the viewing port on the starboard side of the submersible were identified (when possible) and counted.

Two parallel lasers were mounted on either side of the external video camera at a fixed distance of 39.5 cm apart (Fig. 2). The projected reference spots on the video tape, and also visible in situ to the observer, were critical in estimating the size of fishes and distance traveled along a transect. We made measurements by comparing the size of a fish or habitat feature to the known spacing of the two bright laser spots when the object was nearly perpendicular to the camera and lasers (Davis and Tusting 1991). We estimated the length of each transect, independent of submersible speed and bottom currents, by tracking the spacing of the two laser spots along the transect's path. The video tapes were used to supplement in situ observations of the scientist and provide independent estimates of habitat coverage and fish size.

Submersible dives also were made by marine geologists at six sites. Relief, habitat type, size and depth range of features were described; these field descriptions assisted the biologists in planning dives at each site and for post-cruise assessment of habitat. Microhabitat of the dominant fish species was characterized at each site. Substrata type included various combinations of mud, cobble, boulders, and rock ridge. Species-specific abundance at each site was standardized by distance covered during a transect.

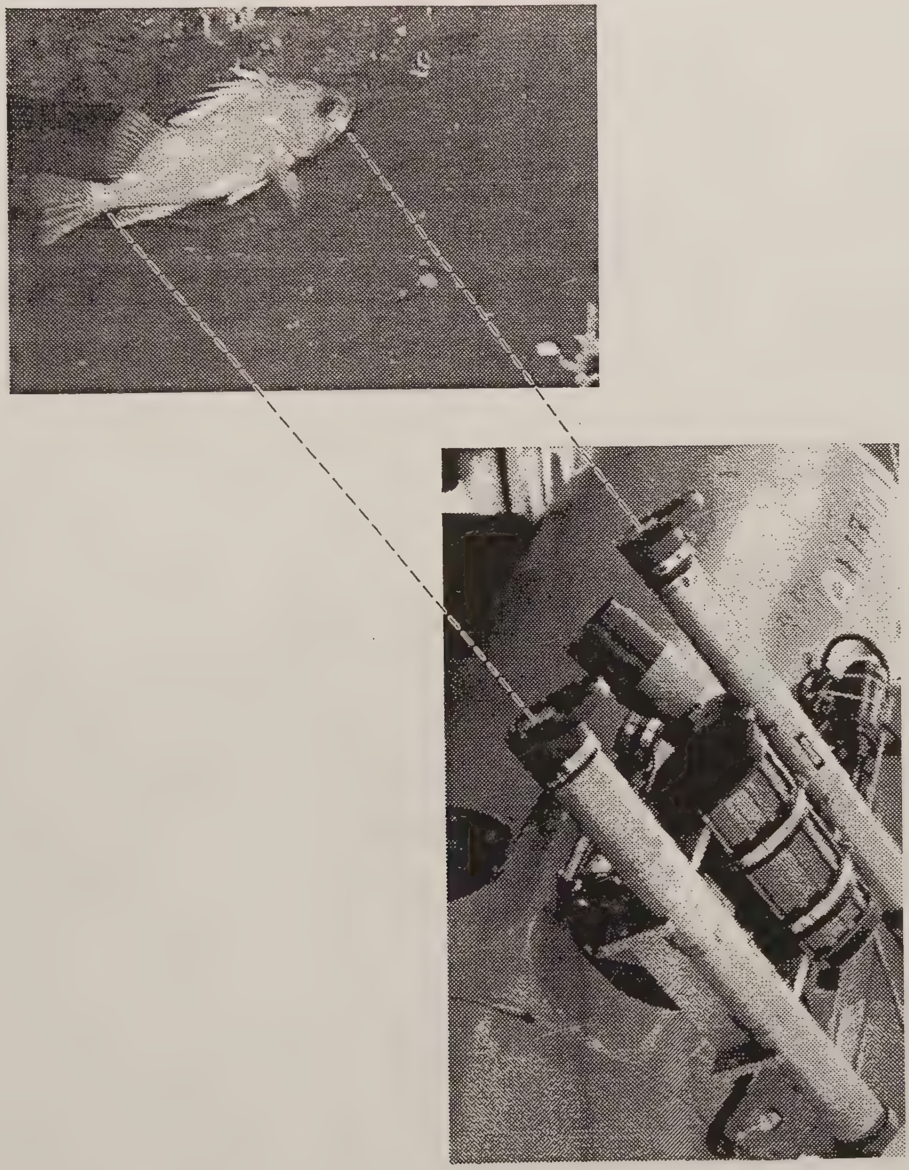

Figure 2. Composite demonstrating (a) the parallel lasers mounted to an underwater camera and used to estimate fish size and distance travelled along transects, and (b) an *in situ* video print of a greenspotted rockfish (*Sebastes chlorostictus*) at interface of boulder and mud substratum (laser spots are evident).

During the third phase, which was concurrent with the submersible operations, we conducted a sidescan sonar survey of Soquel Canyon. Four nights were spent surveying the north end of the canyon, particularly over 80-300 m of water. Side scan sonar is the perfect method for differentiating blocks of hard substrata, which appear dark, from surrounding soft bottom sediments because of their greatly different reflection characteristics (Fig. 3). The sonographs along each track line of the survey were combined with navigational plots from differential Global Positioning System (GPS) to form a mosaic of the canyon walls. When plotted on regional bathymetry, the side scan targets are identified as areas of positive or negative relief. We are using these maps or mosaics to quantify the amount of rocky outcrops available to rockfishes. Our interpretations of the sonographs were verified by observations made from the *Delta* submersible.

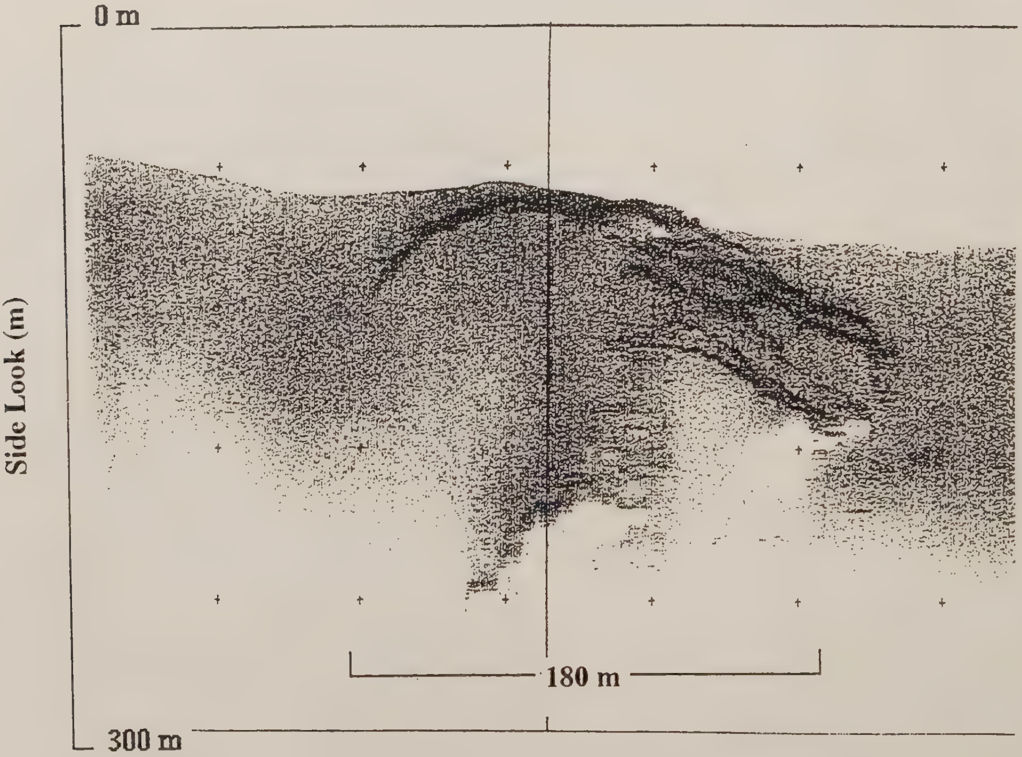

Figure 3. Side scan sonograph of outcrop on wall of Soquel Canyon. Strong acoustic reflectors are from exposed bedding faces, white areas are shadows behind faces, and gray areas are the result of non-reflective muds. These beds, primarily sandstone and mudstone, compose the rockfish habitat. These interpretations were verified by direct observations from submersible.

## RESULTS AND CONCLUSIONS

From the geophysical surveys and observations made during seven geological dives at six sites, Soquel Canyon is characterized by extensive erosion, with sharp, steep relief in much of the headward part. This particular geomorphology is thought to have been created by marine and river erosion during the last low-stand of sea level (H. G. Greene, USGS, Menlo Park, CA, pers. comm.). This canyon is made of many isolated rock outcrops that provide ideal shelter for large fishes.

Twenty-three biological dives were made at eight sites during the pilot study in Soquel Canyon. Five of these sites, in particular, have been verified as excellent rockfish habitat from visual observations using the submersible *Delta*. From post-cruise analysis of 42 10-min transects representing 7.1 km total distance covered, we observed 2,470 individual fishes from 37 species, of which over 2,000 from 21 species were rockfishes. The major rockfish habitat types in Soquel Canyon include vertical cliffs with joints, fractures, and overhangs, small and large ledges, talus slopes and boulder fields of exposed sandstone and mudstone interspersed with soft mud and crinoid fields.

Clustering analysis of all bottom types based on relative abundance of fish species indicates habitat partitioning. Small species, such as sharpchin (S. zacentrus), stripetail (S. saxicola) and halfbanded rockfish (S. semicinctus), were associated with mud and cobble substrata of low relief. Mud-rock combinations were dominated by greenspotted rockfishes (S. chlorostictus; Fig. 2) and an assortment of larger species (e.g., bocaccio, S. paucispinis). The largest species up to 1 m in length, such as cowcod (S. levis) and yelloweye rockfish (S. ruberrimus), were closely associated with larger structures such as rock ledges, small caves, crevices, and overhangs. Many rockfishes of all sizes were associated with some structure, including boulders, cobble, invertebrates such as crinoids and sea anemones, debris, and simple shallow depressions in the mud. In seeking shelter near rock outcrops, large rockfishes may be excavating the friable semi-consolidated mudstone; this type of bioerosion could result in some of the geologic characteristics of the habitat.

From our pilot study, the preliminary conclusion is that heterogeneous, rocky habitat of high relief surrounded by soft mud in deep water of submarine canyons supports viable adult rockfish populations. These fishes are likely protected from excessive harvest because these habitat characteristics make them difficult to target. Indeed, species and size composition of rockfishes in the catch of the recreational fisheries in the Soquel Canyon area are very different from assemblages described from our submersible observations at similar depths and locations (Fig. 4). The more mobile species (e.g., chilipepper, S. goodei, and yellowtail rockfishes, S. flavidus) that tend to aggregate off the bottom may be more vulnerable to the hook-and-line fisheries, whereas the larger benthic species (cowcod, yelloweye rockfish, and lingcod) are relatively more abundant in the submersible observations.

Because of the many canyon systems in or near Monterey Bay, deep-water rocky habitats are accessible relatively close to heavily-fished areas, making comparisons among sites possible. From our fishery-independent estimates of rockfish abundance and habitat availability and characterization, we can evaluate the need for protecting populations of rockfishes on small-scale refugia. These areas could serve as sources of recruitment for fish populations being reduced by fishing, and identifying critical habitat for mature adults could prevent further declines in population numbers of some species.

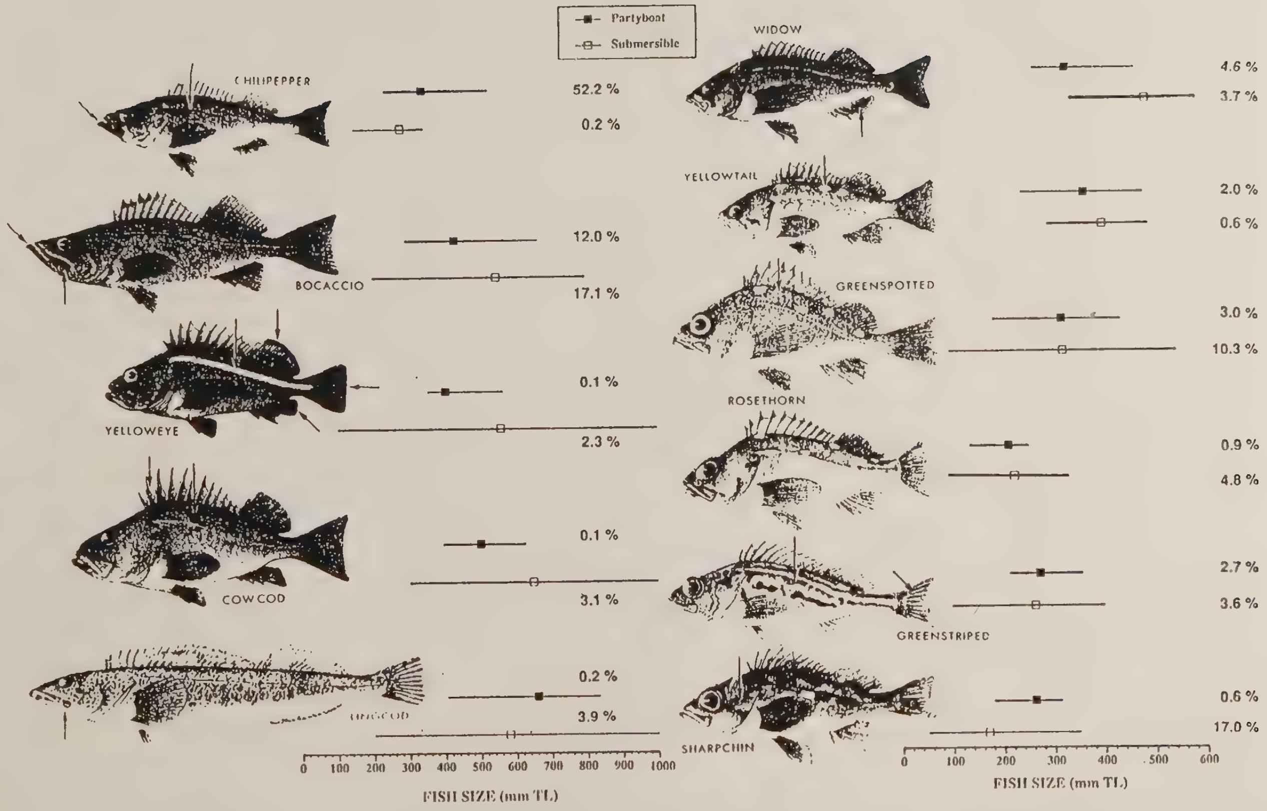

Figure 4. Many species of rockfishes are relatively more abundant and larger in Soquel Canyon than indicated in catch records. Percent abundance, mean and range of sizes are indicated for fishes caught by partyboat fleet and observed during submersible surveys at 90-209 m in Soquel Canyon. Illustrations are from Eschmeyer, Herald, and Hammann (1983).

Our observations demonstrate the utility of submersibles for evaluating fish populations that are closely associated with deep-water rocky areas and unavailable to other methods of evaluation. Manned submersibles provide the scientists with superior field of view to directly quantify abundance and size, and identify difficult species. The high resolution video camera produces a continuous record of observations and allows observers to review their rockfish identifications. Submersible techniques are ideal for surveying potential small-scale refugia without altering the population parameters being quantified.

## FUTURE RESEARCH

We are continuing our study of submarine canyons in the Monterey area to compare fish assemblages in lightly- and heavily-fished habitats of similar type and depth. From our recent geophysical survey, we are identifying likely rockfish habitat along the south edge of Monterey submarine canyon and on isolated outcrops in the bay. These ledges have been accessible to substantial and continuous fishing pressure in Monterey Bay for several decades. Using transect techniques and the *Delta* submersible, we will survey fish populations, and compare species and size composition to those from catch records collected by CDFG observers on board Commercial Partyboat Fishing Vessels in the area.

We are currently assessing the likelihood that submarine canyons having structure similar to Soquel Canyon represent significant habitat for rockfishes. Geologic characterization of the headward parts of Monterey, Ascension, Ano Nuevo and Carmel Canyons (particularly from 100-350 m water depth) is in progress, with direct observations from a submersible planned for summer of 1994.

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